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Part 1
Lake Huron and Saginaw Bay

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A mathematical model of phytoplankton biomass was developed which incorporates both phytoplankton and zooplankton as well as phosphorus, nitrogen and silica nutrient forms. Extensive water quality data for Lake Huron and Saginaw Bay was analyzed and statistically reduced. The model was then calibrated by comparison of computed results to these data.

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MATHEMATICAL MODELS OF WATER QUALITY IN LARGE LAKES
PART 1: LAKE HURON AND SAGINAW BAY

by

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FOREWORD

The Great Lakes comprise 80% of the surface freshwater in North America and provide 45 million people living in the basin with almost unlimited drinking water and industrial process water. Five thousand miles of shoreline provides access for much of the tourist and recreation activity in the surrounding basin. Lucrative sport and commercial fisheries rely on these waters as do the transport of tremendous quantities of raw and refined commercial products and the disposal of residual, industrial and municipal materials.

This resource represents a complex system of competing water uses as well as a delicate, interacting ecosystem. Such a situation requires a balance between the economic well being of the region with the health related well being of the ecosystem. To arrive at this balance a rational and quantitative understanding of the interacting and competing components is required. In this way complex questions can be addressed and optimal decisions made.

Research sponsored by the U.S. EPA, ERL-D, Large Lakes Research Station has in large part been directed toward this end. Primarily the modeling research has been conducted to synthesize surveillance and research data and to develop predictive capabilities of the transport and fate of pollutants in the Great Lakes.

This report documents the results of a three year research project to develop a water quality model for Lake Huron and Saginaw Bay. The purpose of including the kinetic formulations, data analysis, and verification procedures is to provide sufficient detail that would not be available in journal publications so that much of this methodology could be applied to other water bodies throughout the world. Also, it is our intent to document the details for those Great Lakes' managers and researchers who have and will develop, recommend and judge pollution control strategies based on this research.

Appreciation is extended to scientific reviewers at the University of Michigan and the NOAA, Great Lakes Environmental Research Laboratory. The report has also received extensive review by several Canadian and State agencies.

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ABSTRACT

This research was undertaken to develop and apply a mathematical model of the water quality in large lakes, particularly Lake Huron and Saginaw Bay (Part 1) and Lake Erie (Part 2).

A mathematical model of phytoplankton biomass was developed which incorporates both phytoplankton and zooplankton as well as phosphorus, nitrogen and silica nutrient forms. Extensive water quality data for Lake Huron and Saginaw Bay was analyzed and statistically reduced. The model was then calibrated by comparison of computed results to these data.

An exhaustive treatment of the kinetics employed for modeling the eutrophication process is presented. The sensitivity of the model to some of its key parameters is examined. In addition, responses of water quality in Lake Huron and Saginaw Bay system to variations in total phosphorus inputs are projected.

This report was submitted in fulfillment of Grant No. R803030 by Manhattan College under the sponsorship of the U.S. Environmental Protection Agency. This report covers the project period March 26, 1974 to March 25, 1977.

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This study could not be undertaken without adequate data to serve as input and for calibration purposes. We therefore extend special thanks to the Cranbrook Institute of Science, the Canada Centre for Inland Waters, and the Great Lakes Research Division of the University of Michigan for supplying and permitting us to use their water quality data. The cooperation of all members and committees of the Upper Lakes Reference Group of the International Joint Commission, particularly those who provided us with waste loading information, is also gratefully acknowledged.

The participation, helpful criticism, and support of our colleagues at Manhattan College: Robert Thomann and Donald O'Connor, and at the EPA Grosse Ile Laboratory: Nelson Thomas, William Richardson, Victor Bierman, and Tudor Davies (presently of EPA, Gulf Breeze, Florida) is greatly appreciated. Special thanks are also due to Mrs. Eileen Lutomski for her typing of the report manuscript.

SECTION 1

INTRODUCTION

The principle objective of this research project is to structure and apply a numerical model of phytoplankton biomass in Lake Huron and Saginaw Bay in order to provide a framework for assessing, managing, and controlling eutrophication problems in these areas of the upper Great Lakes. This work is part of a larger study which also addressed water quality problems in Lake Erie, particularly the depletion of oxygen in the hypolimnetic waters of the Central Basin. Results of that study are reported separately in Part II of this report.

The continuing eutrophication of the Great Lakes, the largest single freshwater system in the world, has been a widely recognized water quality problem. While the open lake waters of Lake Huron are classed as oligotrophic, Saginaw Bay, a shallow, short residence time embayment which serves as a receiving body for a large percentage of the waste loadings entering Lake Huron, is a highly eutrophic area exhibiting, for example, phytoplankton chlorophyll concentrations which are an order of magnitude greater than those found in Huron's open lake waters. Recognizing the potential for large scale water quality deterioration, the International Joint Commission appointed a special committee in April, 1972, the Upper Lakes Reference Group, to determine whether the waters of Lakes Superior or Huron were being polluted on either side of their respective international boundaries to an extent likely to cause a degradation of existing levels of water quality in the Great Lakes system. While this project did not form a part of the Upper Lakes Reference Study, *per se*, it does provide a framework for responding to the reference questions raised therein.

The computation comprises a kinetic structure which characterizes the interrelationship between phytoplankton, herbivorous and carnivorous zooplankton, ammonia, nitrate, and unavailable nitrogen, dissolved ortho and unavailable phosphorus, and silicate. These constituents form the nine dependent variables. This formulation is then coupled to the water transport in the Saginaw Bay/Lake Huron system, the boundary concentrations and nutrient waste loadings. A new framework is developed which relates the rate of recycle of nutrients from unavailable to available inorganic forms to the phytoplankton biomass concentrations. The model is calibrated by comparing computed concentrations to observations. Sensitivity analyses are presented which indicate the extent to which the model's computations depend upon values chosen for key parameters which affect the kinetic interactions of the various model compartments. Finally, applications of the model are presented which project water quality responses in southern Lake Huron and Saginaw Bay to various management strategies for reducing total phosphorus inputs to this system.

SECTION 2

SUMMARY AND CONCLUSIONS

This research project develops a framework for an analysis of the causes and remedies of eutrophication of Lake Huron and Saginaw Bay. The methodology employed is based on a mathematical model which expresses in quantitative terms the mass balance relationships which interrelate the nutrient mass discharges to the lakes, the nutrient concentration in the lake, the phytoplankton and zooplankton response to these nutrients, and their resulting seasonal distribution. The model calculations provide the method by which the fate and impact of present and projected levels of nutrient discharges can be evaluated in terms of their effect on the biomass of phytoplankton. It is for this specific purpose that they have been constructed: to provide a quantitative method by which nutrient management plans can be evaluated.

It is concluded, based on this investigation, that the phytoplankton biomass, nitrogen and phosphorus concentrations in Lake Huron and Saginaw Bay can be adequately modeled using the formulation presented. This is suggested by the fact that the computations reproduce observed concentrations fairly well in both Saginaw Bay and the open waters of Lake Huron where concentrations of most variables span almost an order of magnitude and conditions range from eutrophy to oligotrophy.

Mass balance calculations are based on three components: estimates of the rate of nutrient mass discharges to the lake; estimates of the vertical and horizontal transport regime; and estimates of the nutrient, phytoplankton, and zooplankton kinetics. This report is concerned with the latter two components; the mass discharge rates have been estimated by the Upper Lakes Reference Study group. [98] The mass balance calculations are made for each

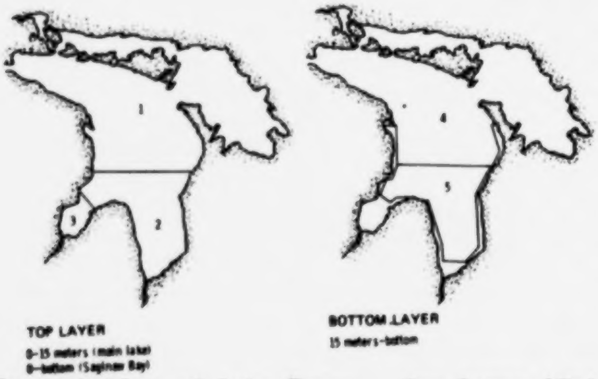


Figure 1. Segmentation of Lake Huron. Top Layer (Epilimnion) and Bottom Layer (Hypolimnion) of Northern and Southern Lake Huron. Segment 3 represents Saginaw Bay.

of the five segments, illustrated in fig. 1, which represent the epilimnion and hypolimnion of Northern and Southern Lake Huron, and Saginaw Bay. The transport regime between these segments is evaluated using convenient conservative tracers, primarily temperature. As shown in fig. 2 the vertical exchange coefficient is established from the seasonal distribution of temperature. The lines in the figure are the result of a temperature balance calculation employing the vertical exchange coefficient illustrated in the figure. A similar calculation for Saginaw Bay using both temperature and chloride concentration establishes the horizontal exchange between Saginaw Bay and Southern Lake Huron.

The kinetics of the computation are illustrated in fig. 3. The phytoplankton are represented by their chlorophyll concentration; the zooplankton are partitioned into herbivorous and carnivorous groups. The two major nutrient cycles considered are the phosphorus and nitrogen cycle. Both unavailable and available forms are considered and as shown subsequently the rate of recycle of unavailable to available phosphorus is a focal point of the analysis. These kinetics are expressed in mathematical terms and, together with the transport regime and the mass discharges, they comprise the mathematical model that is the basis of the calculation.

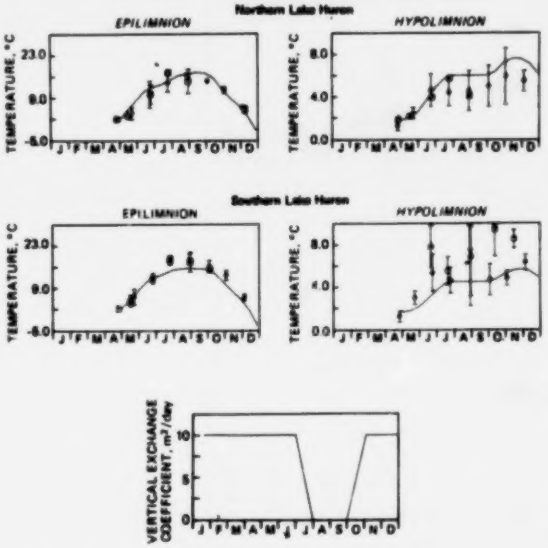


Figure 2. Vertical Transport Calibration

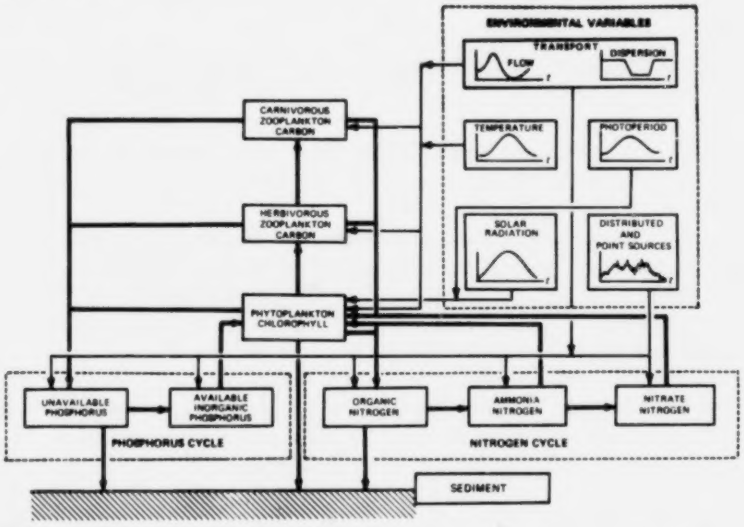

ENVIRONMENTAL VARIABLES
TRANSPORT
FLOW
DISPERSION
TEMPERATURE
PHOTOPERIOD
SOLAR RADIATION
DISTRIBUTED AND POINT SOURCES
t
CARNIVOROUS ZOOPLANKTON CARBON
HERBIVOROUS ZOOPLANKTON CARBON
PHYTOPLANKTON CHLOROPHYLL
UNAVAILABLE PHOSPHORUS
AVAILABLE INORGANIC PHOSPHORUS
PHOSPHORUS CYCLE
ORGANIC NITROGEN
AMMONIA NITROGEN
NITRATE NITROGEN
NITROGEN CYCLE
SEDIMENT

Figure 3 Schematic Diagram of the Kinetic Interactions

The critical step in the development of this or any model is calibration: the comparison of computed concentrations for each of the nine variables considered in each of the five segments of the lake. The ability of the model to reproduce present conditions is a necessary prerequisite in establishing its validity. An example of the calibration results for Saginaw Bay and the Southern Lake Huron epilimnion is shown in fig. 4. The concentrations of nutrients and phytoplankton in these regions are quite different: Saginaw Bay is almost an order of magnitude more enriched in phosphorus and chlorophyll than the main lake and the computation responds accordingly. These and the other calibration results are used to assess the probable range of applicability of the model to projected conditions. In particular the calibration and other analyses described in section 6 indicate that the recycle rate in Southern Lake Huron is considerably slower than in Saginaw Bay. The effect has important implications in the projected response of Lake Huron to increased phosphorus discharges.

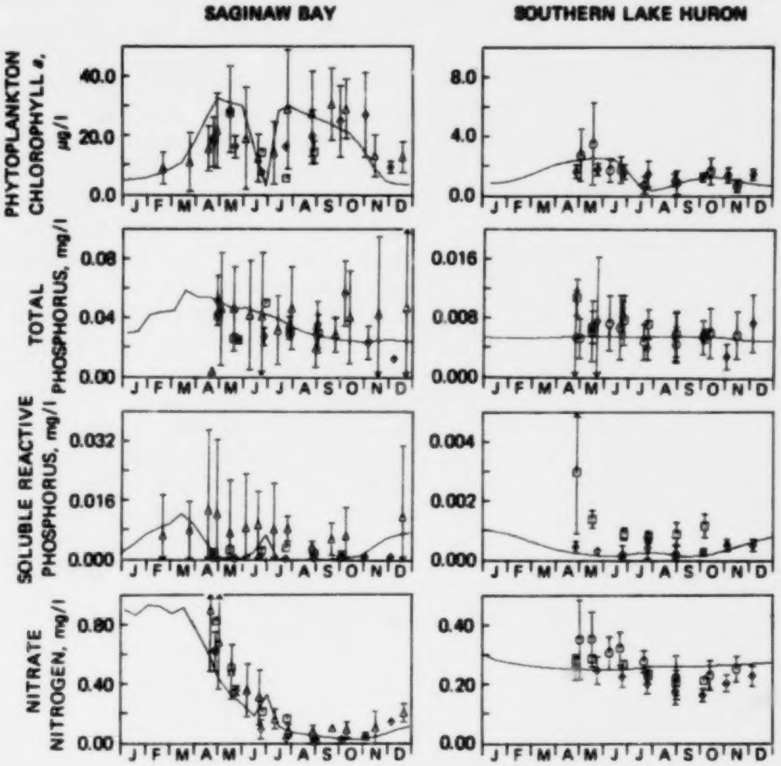


Figure 4. Results of model calibration: Computed versus Observed Data in Southern Lake Huron and Saginaw Bay.

In order to further verify this phenomenon a previous analysis of Lake Ontario was modified to include this new recycle rate formulation. The

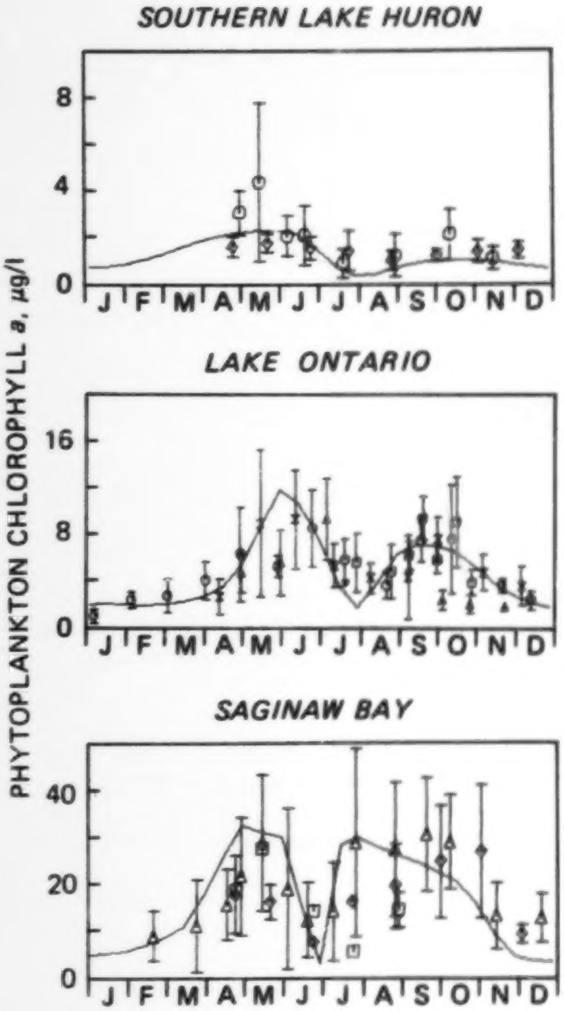


Figure 5. Final calibration computations for Southern Lake Huron, Lake Ontario, and Saginaw Bay phytoplankton chlorophyll.

result is that it is possible to reproduce the phytoplankton chlorophyll and nutrient seasonal distributions for Southern Lake Huron and Lake Ontario epilimnia and Saginaw Bay using the same phytoplankton and nutrient kinetic structure and constants as shown in figure. 5. This simultaneous applicability suggests that the model employed in this calculation has a more general validity and its use in making projections is supported.

A sensitivity analysis is presented in order to assess the effects of varying kinetic constants on the computation. In particular it appears that although the shape of the seasonal distribution is strongly affected by the zooplankton kinetics the peak and yearly average concentrations are rather insensitive. Therefore the projections for these measures of eutrophication are not invalidated by the uncertainties in the zooplankton kinetic coefficients.

Projection calculations for various phosphorus mass discharge rates are presented in section 10, an example of which is shown in fig. 6. The importance of phosphorus recycle is shown in the projected yearly average chlorophyll change to be expected from changes in yearly average phosphorus inputs. For saturation kinetics, which are suggested by the calibration results, a doubling of the phosphorus loading is projected to increase the yearly average chlorophyll over 300% whereas for first-order recycle a doubling would be projected. This implies that Southern Lake Huron is quite senstive to changes in phosphorus loading and it would respond more dramatically than strictly linearly to increases in phosphorus inputs. More detailed projection calculations including Saginaw Bay are included in section 10. The results indicate than an annual load of total phosphorus to Lake Huron of 3600 metric tonnes/yr. will maintain existing chlorophyll levels in Southern Lake Huron achieving non-degradation. It is also projected that phosphorus reductions at municipal sewage treatment plants in the Saginaw Bay area to effluent concentrations of 1 mg/ℓ which will reduce the Saginaw Bay load by 600 tonnes/yr. will result in yearly

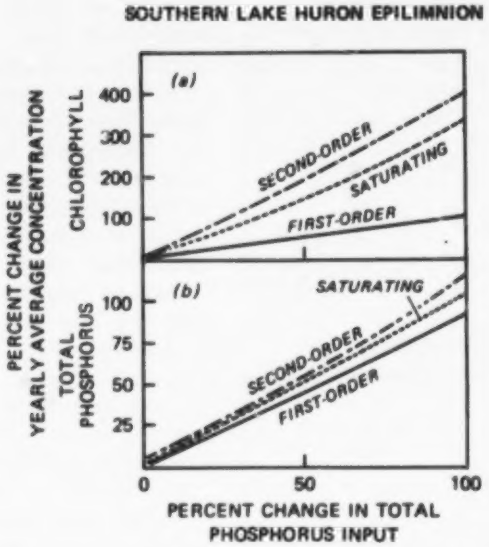


Figure 6. Effect of Increases of Phosphorus Inputs to Southern Lake Huron. Percent change in yearly average epilimnion concentration versus percent change in total phosphorus input (a) Chlorophyll, $\underline{P}$; (b) Total phosphorus, p_T.

average chlorophyll concentrations of about 1.1 µg/ℓ in Southern Lake Huron and 10.7 µg/ℓ in Saginaw Bay. These results have been used by a United States-Canadian Task Group for purposes of developing total phosphorus loading objectives to the Great Lakes as part of the re-negotiation of the 1972 Water Quality Agreement [104].

SECTION 3

RECOMMENDATIONS

Due to the significance of the role which nutrient recycle plays in the Lake Huron and Saginaw Bay ecosystem, experimental investigations should be undertaken to provide additional insights into the factors affecting these mechanisms. Furthermore, since classical phytoplankton growth kinetics do not reproduce well what appears to be significant observed chlorophyll a concentrations in the cold and dark hypolimnion waters of Southern Lake Huron, further studies of this deep chlorophyll phenomenon are recommended to determine whether, for instance, low light adaptation, transport, migration, or some combination thereof contributes to this observed effect. In addition, a verification of the model developed hereunder should be performed utilizing Saginaw Bay waste loadings which were lowered subsequent to this study as part of a remedial phosphorus reduction program. Some long term model simulations incorporating yearly variations in waste loading are also recommended to determine if present observations can be reproduced. Such verification exercises would provide an additional degree of validity to the model as it presently stands.

SECTION 4

PHYSICAL FEATURES, MASS LOADINGS, AND SEGMENTATION

A major legacy of Pleistocene glaciation is the formation of the Great Lakes [1], the largest freshwater system on earth. Lake Huron is the second largest of these Great Lakes and is the fifth largest lake in the world [2]. Saginaw Bay is an inland extension of the western shore of Lake Huron projecting southwesterly midway into the southern peninsula of Michigan [3].

Lake Huron is connected to Lake Michigan by the Straits of Mackinac, to Lake Superior by the St. Mary's River, and to Lake St. Clair by the St. Clair River. Lake Huron with Saginaw Bay and the combined drainage basin is shown on fig. 7.

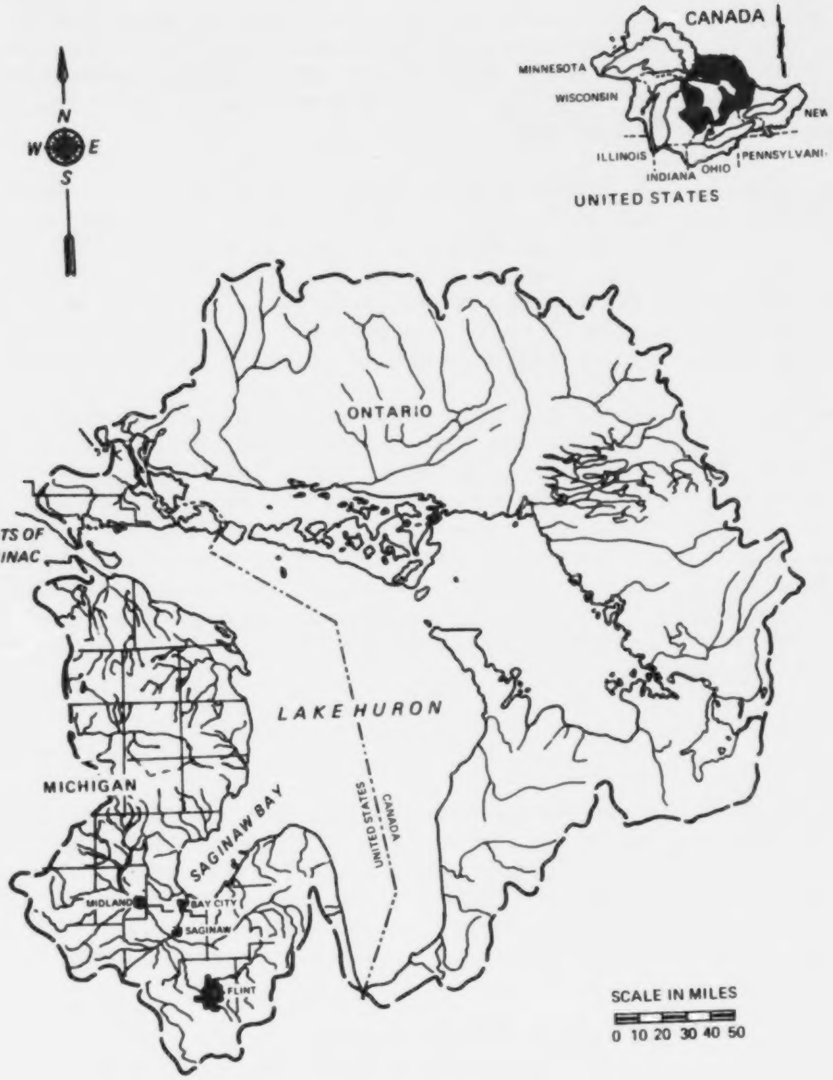
GEOMORPHOLOGY

Lake Huron's water surface is 176 meters (579 feet) above sea level. The total water surface area, including Georgian and Saginaw Bay, is 59,570 km^2 (23,000 mi^2) [4,5]. The lake drains a total land and water area of 193,700 km^2 (74,800 mi^2) [4], two-thirds of which is land drainage. Measured from low water datum, Lake Huron has a maximum depth of 229 meters (750 feet) [4]. Averaged over the lake, the mean depth is reported as 53-59 meters [4,5]. Total water volume of Lake Huron is 3535 km^3 (848 mi^3) [4,5]. The length of the lake is 330 km (205 miles) with its breadth being 292 km (181 miles) [5]. Total shoreline including islands is 5,088 km (3162 miles) [5].

Saginaw Bay is a shallow arm of Lake Huron 42 km (26 miles) wide and approximately 82 km (51 miles) long. The bay's 2960 km^2 (1143 mi^2) of surface area are equally divided between an inner and outer bay divided by a constriction where the bay narrows to 21 km (13 miles). The shallower inner zone has a mean depth of 4.6 meters (15 feet) while the outer bay mean depth if 14.6 meters (48 feet). The maximum depth is 40.5 meters (133 feet) in the outer bay [3].

HYDROLOGY

Lake Huron is in the central portion of the Great Lakes Basin, southeast of Lake Superior and east of Lake Michigan. It receives outflow from Lake Superior through the St. Mary's River, a channel 112 km (70 miles) long. Lake Huron also receives outflow from Lake Michigan via the Straits of Mackinac. The straits of Mackinac provide a broad and deep connection between Lake Michigan and Lake Huron, being more than three miles wide at


CANADA
MINNESOTA
WISCONSIN
NEW
ILLINOIS
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OHIO
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STRAITS OF MACKINAC
LAKE HURON
MICHIGAN
SAGINAW BAY
MIDLAND
BAY CITY
SAGINAW
FLINT
UNITED STATES
CANADA
SCALE IN MILES
0 10 20 30 40 50

Figure 7. Lake Huron and Saginaw Bay Drainage Basin

their narrowest point and ranging in depth to more than 61 meters (200 feet). Direction of currents in the Straits alternates from east to west depending upon meteorology. Net flow, however, is to Lake Huron [4]. It should be noted, however, that flow reversal with depth during the stratified season has been observed in the Straits of Mackinac [100]. This phenomena, in turn, has been determined to have a significant effect on the estimation of transport through the Straits [101]. Outflow from Lake Huron is via the St. Clair River at its southernmost tip.

The average flow (1860-1970) to Lake Huron from the St. Mary's River draining Lake Superior is 2123 m^3/sec (75000 cfs). The flow across the Straits of Mackinac from Lake Michigan is estimated to be 1472 m^3/sec (52,000 cfs); while that leaving via the St. Clair River is 5,303 m^3/sec (187,300 cfs) [4]. The average annual precipitation (1900-1970) on Lake Huron's water surface is 79 cm (31 inches) [4,5], and the average annual evaporative loss has recently been estimated at 66 cm (26 inches)[4].

The Saginaw River is the major source of drainage flowing to Saginaw Bay. Formed by the convergence of the Shiawassee, Tittabawasee, Cass, and Flint Rivers, the Saginaw River is 35 km (22 miles) long and enters the bay at its southwestern end. The average annual water levels in Saginaw Bay are controlled by the Lake Huron water level. The bay itself, however, exhibits very short term, rapid and large fluctuations as a result of wave runup, wind driven tides, and seiches [3]. Some of these propagate down the Saginaw River and cause flow reversal. Flows typically range from 14 to 227 m^3/sec (500 to 8000 cfs) throughout a year with an average value estimated to be 109 m^3/sec (3850 cfs) [3].

MASS INPUTS

The earliest comprehensive mass loading data for Saginaw Bay is available from the 1965 survey by the FWPCA of Michigan tributaries. They are based on Saginaw River and other bay tributary measurements of total and ortho phosphorus, and nitrate, ammonia and organic nitrogen. No Lake Huron estimates for the comparable period are available, however. Johnson [6] summarizes some typical Saginaw Bay loadings from its major tributaries based on the 1965 surveys.

The Great Lakes Water Quality Board [7,8,9] has made estimates of the 1972 to 1974 overall lake loadings for total phosphorus and total nitrogen. Estimates of loadings under reduction policies are also included. The breakdown of the total nutrient loading into various nitrogen and phosphorus forms and their spatial distribution are not estimated.

In view of the lack of comprehensive and detailed mass loading information for Lake Huron and Saginaw Bay, a major effort was instituted in order to rectify this situation. As part of the Upper Lakes References Study of the IJC, one of the aims of which is to document the present water quality status of Lake Huron, "data collection programs and studies were proposed for the purpose of determining the loading of materials to the lakes which could adversely affect their water quality" [10]. Sources studied included municipal, industrial and tributary point sources as well as other land and atmospheric inputs (nonpoint sources). These studies provide the necessary comprehensive mass loading data without which it is impossible to perform meaningful mass balance calculations.

In addition to total nutrient mass loading information it is necessary to know the forms of the nutrient, the important division being available or unavailable for phytoplankton growth. The division into the various nutrient forms: ammonia, nitrite plus nitrate, and organic for nitrogen; and soluble reactive and unavailable (total minus reactive) for phosphorus, were determined based on information which was available for Province of Ontario and State of Michigan tributary loadings. Atmospheric loads were evenly divided between ammonia and nitrate for nitrogen, while all atmospheric phosphorus was considered to be in the soluble reactive form.

For Lake Huron proper, average annual mass loadings suffice because of its large volume and long residence time for nutrients. However for Saginaw Bay more detailed information is necessary, since the bay is highly responsive. Based on the 1974 surveys of Saginaw Bay (Section VI), which had a few stations at the mouth of the Saginaw River, USGS flow data, and State of Michigan water quality stations, Richardson and Bierman [11] computed loadings to Saginaw Bay from the Saginaw River, its major contaminant source. Figure 8 shows these loadings as a function of time together with the Saginaw River flow. As can be seen, all parameters are highly correlated to the flow, as would be expected, with spring runoff flows yielding the highest loading rates. Flow is relatively small in the latter half of the year as are the loadings.

The mass loading estimates used in the subsequent calculations are a combination of the Lake Huron loadings computed by the Upper Lakes Reference Group and the time variable Saginaw Bay loadings. Both are computed using 1974 data. Table 1 summarizes the total nitrogen and phosphorus loadings which are used in the Lake Huron/Saginaw Bay computation.

TABLE 1. NUTRIENT LOADINGS

Location	Total Phosphorus (tonnes/yr)	Total Phosphorus (lbs/day)	Total Nitrogen (tonnes/yr)	Total Nitrogen (#/day)
Northern Lake Huron	1,281	(7,739)	58,186	(357,441)
Southern Lake Huron	1,297	(7,832)	35,773	(216,066)
Saginaw Bay	1,315	(7,945)	17,678	(106,773)
TOTALS	3,893	(23,516)	111,637	(674,280)

SEGMENTATION

Five segments are chosen to represent the significant regions of the Lake Huron - Saginaw Bay system described in the preceding section. The

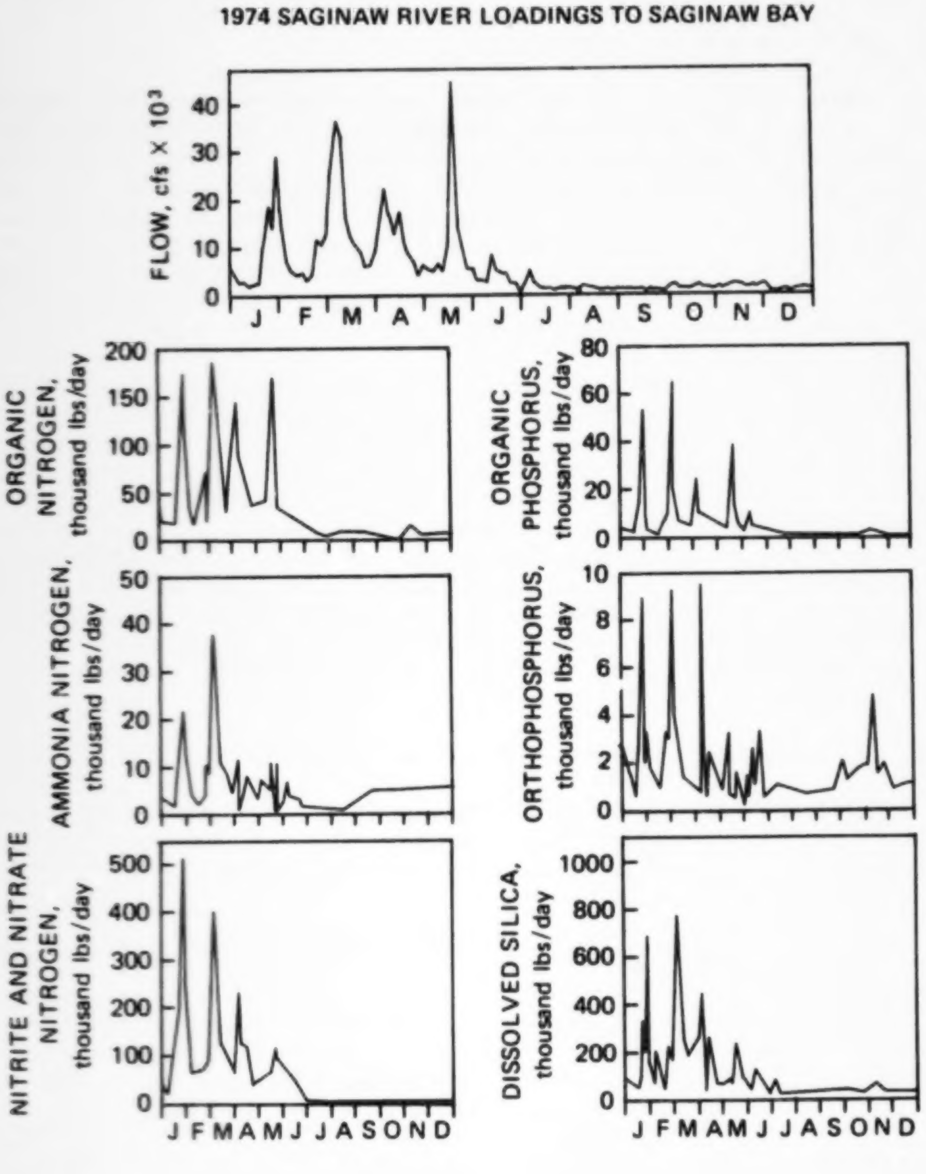


Figure 8. Annual distribution of Saginaw River flow and nutrient mass loading rates, 1974.

choice is a compromise between a realistic characterization of the major features of the biological and chemical variations and the constraints of computation and simplicity, with the emphasis on the latter requirements.

Three surface segments are considered: Northern Lake Huron, a large open expanse of water which tends to be deeper and colder than other portions of the lake and receives the inputs from Lake Superior and Lake Michigan and from major Canadian tributaries feeding the North Channel and Georgian Bay; Southern Lake Huron bounded by the Canadian and Michigan shorelines which approach one another to form the St. Clair River outlet channel. It is influenced, to some degree, by the Saginaw Bay flow sweeping down its western shoreline. Concentrations of biological and chemical parameters tend to be slightly higher than in the open lake waters to the north. Saginaw Bay receives the loading from the Saginaw River. Its waters are significantly enriched as compared to the oligotrophic waters of the rest of Lake Huron.

Figure 9 presents the segmentation. Segment 1 encompasses the northern Lake Huron epilimnion. Its depth ranges from the surface to 15 meters (49.2 feet) which is the approximate thermocline depth as well as the euphotic zone depth (1% surface light penetration depth). The lower boundary of segment 1 is the line of 44° 30' north latitude or roughly a line across the lake connecting a point 8 km (5 miles) north of Oscoda on the Michigan shoreline to a point just north of Southhampton on the Province of Ontario shoreline. Georgian Bay and the North Channel are not included as part of the segment.

The epilimnion of southern Lake Huron comprises segment 2, also 15 meters deep. It is bounded to the north by segment 1 and it also interacts with the Saginaw Bay model segment to the west. Segment 2 is the outflow segment as its southern boundary is the St. Clair River outflow channel.

Segments 4 and 5 comprise the northern and southern Lake Huron hypolimnion, respectively. They are both 50 meters (164 feet) deep and are situated directly below their respective epilimnion segments with their outer ring boundary being the 15 meter depth contour of the lake. Together, they form the second vertical layer of the model. Inclusion of hypolimnetic segments is required to characterize the thermocline formation, its effects on vertical transport, and the effect of phytoplankton sinking and net transport of biomass and associated nutrients to the sediment.

Saginaw Bay is represented by segment 3. It encompasses all of the inner bay and part of the outer bay. The mean depth of this segment is 6 meters (19.7 feet) slightly deeper than the reported inner bay mean depth of 4.6 meters, since some of the outer and deeper portions of the bay are also included. Saginaw Bay is characterized by only one vertical layer since only in the outer reaches of the bay does a well formed thermocline persist in the summer and fall.

Table 2 lists the individual segment depths, surface areas, and volumes. These were obtained by using navigational charts [12,13], measuring the areas of concern with a planimeter, and converting using map scales. When the volumes for the North Channel and Georgian Bay are added to the

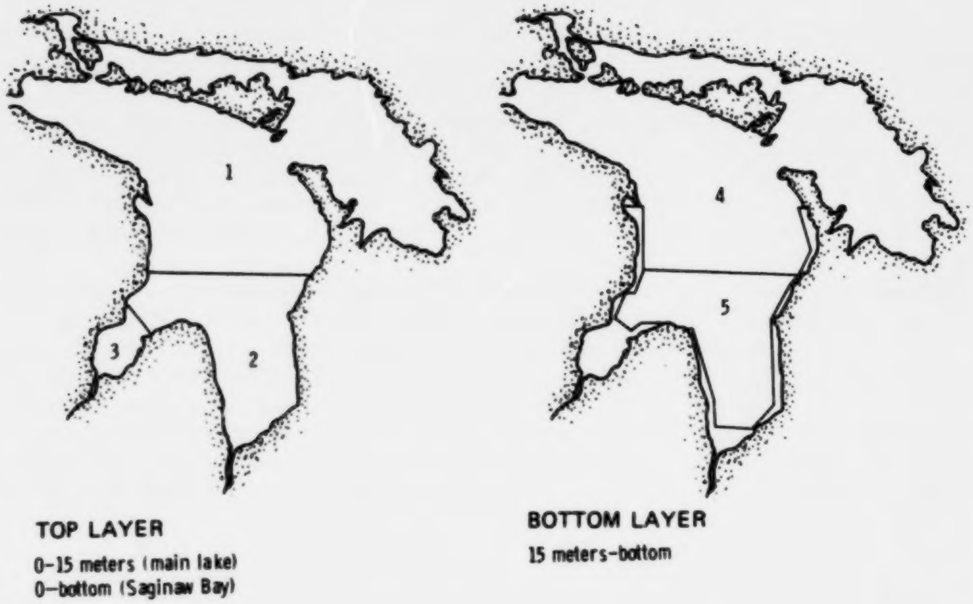

1
2
3
4
5
TOP LAYER
0-15 meters (main lake)
0-bottom (Saginaw Bay)
BOTTOM LAYER
15 meters-bottom

Figure 9. Segmentation of Lake Huron. Top Layer (Epilimnion) and Bottom Layer (Hypolimnion) of Northern and Southern Lake Huron. Saginaw Bay is represented by one layer.

total values for the five segments the result is within 3.5% of reported values [4,5] for total lake volume.

TABLE 2. SEGMENT PARAMETERS

Segment	Depth meters	(feet)	Surface Area km^2	(mi^2)	Volume km^3	(mi^3)
1	15	(49.2)	24,882	(9,608)	373.4	(89.6)
2	15	(49.2)	14,780	(5,707)	221.7	(53.2)
3	6	(19.7)	1,815	(701)	10.8	(2.6)
4	50	(164.1)			1141.1	(273.8)
5	50	(164.1)			619.7	(148.7)
			41,477	(16,016)	2366.7	(567.9)

SECTION 5

ESTIMATION OF THE SEASONAL TRANSPORT REGIME

The available estimates of the nutrient mass discharge rates to Lake Huron and Saginaw Bay are presented in the previous section as well as the relevant geomorphology and hydrology. These provide the volumes, flows, and material input rates to the surface segments. In order to calculate the resulting concentrations, it is necessary to know the transport rate between the segments. Three segment boundaries are considered: the Northern-Southern Lake segment boundary; the Saginaw Bay-Lake Huron boundary, and the thermocline. The estimates of the transport are based on observations of the magnitude and direction of the currents and the analysis of the distribution of conservative tracers. The former are used for the estimate of the Northern-Southern Lake exchange whereas suitable tracers are available for the Saginaw Bay exchange and thermocline transport.

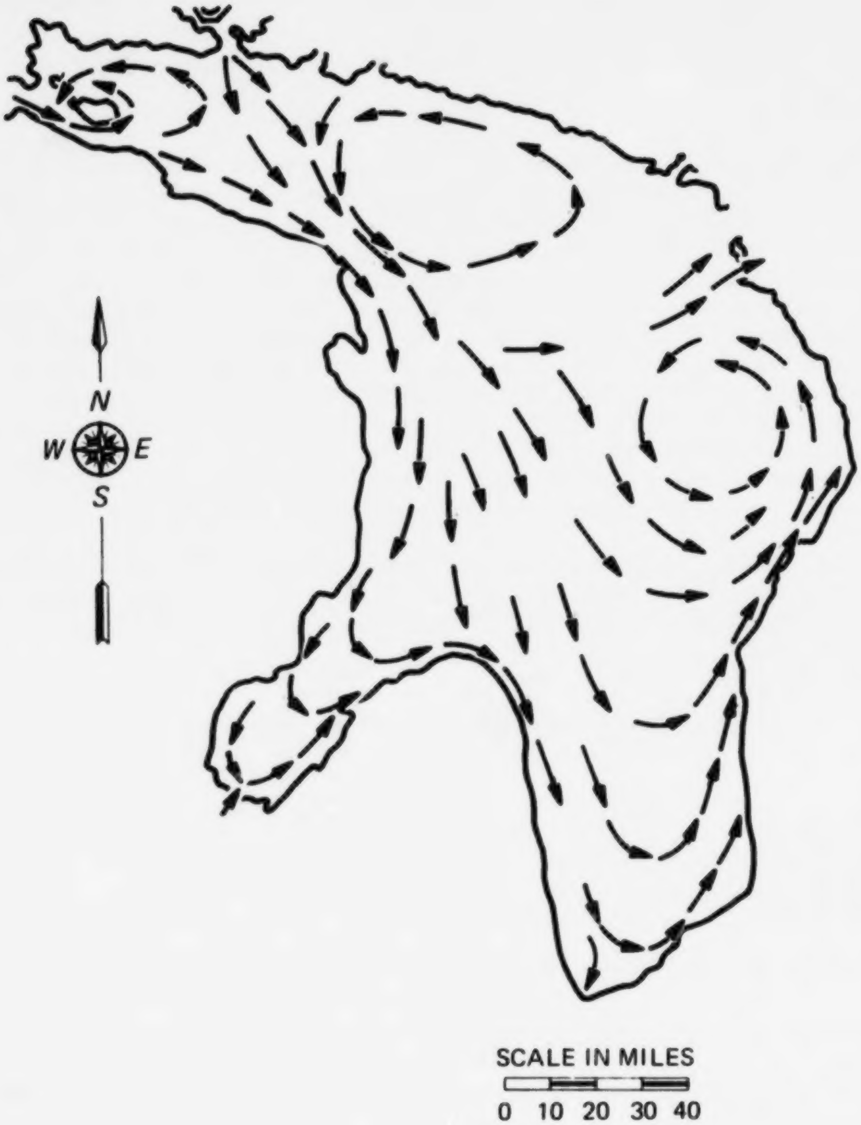
LAKE HURON CIRCULATION PATTERNS

Many factors affect the currents in the Great Lakes. Although primarily wind driven, currents are also affected by temperature, which can form density gradients in the lake; by basin geometry which modifies the currents; by the Coriolis force, an apparent force due to the rotation of the earth; by incoming flows; and by wave effects. A detailed discussion of the complexities involved and governing equations is available [14].

Although current patterns in Lake Huron appear not to be well understood [15], generalized patterns have been observed. Several investigators [6,16,17] have characterized a circulating flow from Lake Huron entering Saginaw Bay at its northwestern shore and exiting along the southeastern shore at least under some prevailing wind direction. Flow from the Saginaw River hugs the southern shore and then exits to Lake Huron [3]. The prevailing circulation seems to be counterclockwise. However, it should be noted that all of the investigators agree that the circulation is sensitive to changes in wind speed and direction which result in short term and rapid fluctuations.

Another major feature of Lake Huron circulation which has been observed is a circulating flow between the northern and southern open lake waters which occurs towards the eastern shore near the center of the lake. Figure 10 illustrates the features of Lake Huron and Saginaw Bay transport described above.

Recent intensive studies undertaken as part of IJC's Upper Lakes Reference Study [102] have significantly enhanced knowledge of Lake Huron currents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E
S
SCALE IN MILES
0 10 20 30 40

Figure 10. Typical surface circulation pattern for Lake Huron (after Ayers et al. (1956) [16]).

especially winter circulation patterns. These winter studies show patterns of flow similar to the circulation of epilimnion water during summer as well as a counterclockwise circulation of waters across the international boundary as shown on fig. 10.

METHODOLOGY

The estimation procedure for transport involves calculating the distribution of suitable tracers and comparing them to observations. This is only possible for the Saginaw Bay exchange with the southern Lake Huron segment since there exist sufficiently large gradients for chlorides, temperature, and total phosphorus. The northern-southern lake circulation is difficult to estimate since no strong gradients exist. The values used are consistent with observed surface velocities [16]. The magnitude of the vertical mixing is established by calibrating a temperature balance calculation to the large gradients which exist between epilimnion and hypolimnion segments. The period of intense stratification, during which no appreciable mixing appears to occur, commences in July and continues through October. Vertical exchanges that are consistent with the temperature observations are determined and used to parametize the seasonal vertical mixing pattern.

The equation which governs the concentration of a conservative tracer in any segment is determined from a mass balance around that segment which takes into account flow into and out of the segment, dispersive exchange, and boundary inputs:

$$V_i \frac{dc_i}{dt} = \sum_j Q_{ij}c_j + \sum_j E'_{ij}(c_j - c_i) + W_i \qquad (1)$$

where: c_i = concentration in the i^{th} segment (M/L^3)
V_i = volume of the i^{th} segment (L^3)
Q_{ij} = volumetric flow rate from segment j to segment i (L^3/T)
E'_{ij} = volumetric exchange rate between segments i and j (L^3/T)
W_i = rate of mass input into the i^{th} segment (M/T)

The flow rates, Q_{ij}, are thought of as the unidirectional flows due to the net advection through the segment boundaries. Thus the Saginaw River flow and the north to south Lake Huron flow described in Section 4, Hydrology, are represented by these terms. The exchange flows are the result of the horizontal circulating flows which are bi-directional, as illustrated in fig. 10, and whatever other mixing processes occur between adjacent segments. For the boundary at the location of the thermocline, the exchange coefficient is related to the vertical dispersion coefficient, E_{ij}, via the expression $E'_{ij} = E_{ij}A_{ij}/\ell_{ij}$ where A_{ij} is the interfacial area and ℓ_{ij} is the length between the segment midpoints [18]. This relationship applies if the segment sizes are small enough so that finite difference approximations to derivatives are reasonable. For the large segments considered in this study, the relationship is only approximate.

The estimation of the Saginaw Bay-Southern Lake Huron exchange coefficient is based on the solution of equation (1) using chlorides as the conservative tracer. In addition, total phosphorus is considered although as shown subsequently some removal occurs due to particulate phosphorus settling. Finally, a temperature analysis is presented to further confirm the estimated exchange rate. The equation used for the chlorides and total phosphorus analysis is:

$$V_3 \frac{dc_3}{dt} = E'_{32}(c_2-c_3) - Q_{23}(t)c_3 + W_3(t) \qquad (2)$$

where $Q_{23}(t)$ is the observed Saginaw river flow and $W_3(t)$ is the observed mass loading rate from the Saginaw River. These are obtained from the EPA and the IJC Upper Lakes Reference Group studies as outlined in Section 4. Comparison to Saginaw Bay loadings calculated by the University of Michigan (Canale, personal communication) are shown on fig. 11. It is interesting to note that the weekly sampling data is necessary to resolve a number of sharp peaks which contribute to the total loading.

The methodology for using temperature as a tracer is a simplification of a full thermal balance calculation. Heat storage in a lake is dependent on many factors including short and long wave solar radiation incident to the water surface; reflected solar radiation; long wave back radiation; sensible heat transfer to the atmosphere; and energy of condensation and evaporation. The net result of these is a net heat flux to the lake which can be thought of as a forcing function for temperature. Thus instead of developing relationships for each of the terms which comprise total heat storage using observations for solar radiation, water reflectivity, air temperature, cloud cover, wind speed, vapor pressure and the like, which is a complex task requiring large amounts of data, heat storage is computed directly from observed temperature data. Mean temperatures for each segment (i) for each cruise (k), T_{ik}, are computed using the 1974 survey data. Because of the relatively uniform spacing of the observations volume-weighted means were a refinement that was judged to be unnecessary. Total heat content change in the lake, ΔH_T, between cruise k and ℓ is then computed using:

$$\Delta H_T = \sum_{i=1}^{n} \Delta H_i = \sum_{i=1}^{n} V_i \, (T_{ik} - T_{i\ell}) \, \rho \, C_p \qquad (3)$$

where:

ΔH_i = change in heat content for the ith segment between cruise k and ℓ (calories)

V_i = volume of segment i (cm^3)

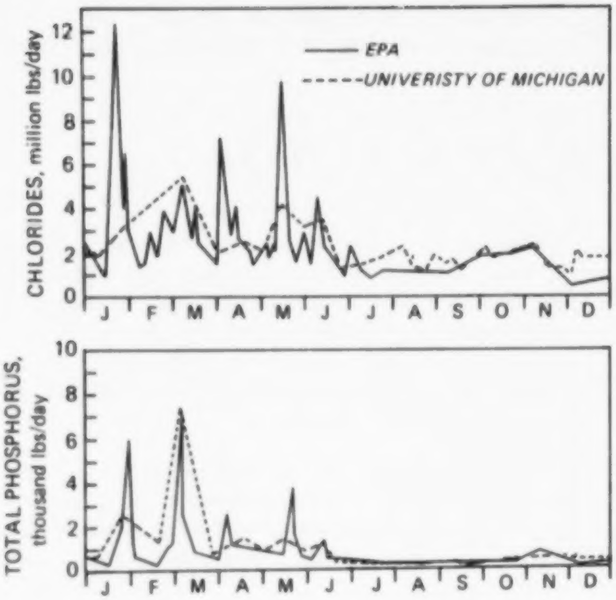


Figure 11. Comparison of Saginaw River mass discharge rates for chlorides and total phosphorus as estimated from weekly and monthly sampling data.

T_{ik} = volume average temperature in segment i on the kth cruise (°C)

$T_{i\ell}$ = volume average temperature in segment i on the ℓth cruise (°C)

C_p = heat capacity of water (cal/g-°C)

ρ = density of water (g/cm^3)

The total lakewide daily average surface heat flux, J_T, between the cruise dates, which represents the net amount of energy input over the surface area of the lake, can then be determined using:

$$J_T = \frac{\Delta H_T}{A_s \Delta t_{k\ell}} \qquad (4)$$

where:

A_s = total lake surface area (cm^2)

$\Delta t_{k\ell}$ = time between the kth and ℓth cruise (days)

J_T = areal heat flux (cal/cm^2-day)

In order to apportion the net heat flux to the surface segments of Lake Huron and Saginaw Bay a number of assumptions are possible. The simplest is to assume that the flux is uniformly distributed over the entire lake. However, certain of the mechanisms which cause this heat flux are dependent on the water surface temperature which is quite different for Saginaw Bay and Lake Huron. Thus a correction for this effect is necessary. The method is based on the assumption that the equilibrium temperature, E, is the same for Saginaw Bay and Lake Huron. This is reasonable since the equilibrium temperature does not depend on the water depth, but only on meteorological variables, which can be presumed to be relatively uniform lakewide. In addition it is assumed that the net heat flux can be computed using a surface heat transfer coefficient coefficient. This approximation can be justified by linearizing the equations for long wave back radiation (Stephan-Boltzman equation) and the equations that depend on the saturated vapor pressure at the water surface temperature [19]. The result is that the net heat flux at location i, J_i, is related to the local surface temperature by the equation:

$$J_i = K(E - T_i') \qquad (5)$$

where:

K = surface heat transfer coefficient (cal/cm^2-day-°C)

E = equilibrium temperature (°C)

T_i' = surface water temperature of segment i (°C)

The prime denotes surface as opposed to volume average temperature. Consider this equation applied to the total lake surface:

$$J_T = \frac{1}{A_s} \sum_i J_i A_{si} K(E-T') \qquad (6)$$

where T' is the lakewide average surface temperature. If it is assumed that the heat transfer coefficient is also constant, for the same reasons that the equilibrium temperature is assumed constant, then a relationship is obtained between the segment specific and the lakewide average heat flux by subtracting eq. (6) from eq. (5):

$$J_i = J_T - K(T_i'-T') \qquad (7)$$

The correction depends on knowing the segment average and lakewide average surface temperatures, which are available from the cruise data, and the surface heat transfer coefficient. For Lake Huron it has been estimated to be $K = 50\text{-}65$ cal/cm^2-day-°C [20]. In units comparable to surface gas transfer coefficients this corresponds to $K/\rho C_p = 0.5 - 0.65$ m/day. The computed lakewide and segment specific heat fluxes resulting from application of this procedure are given in Table 3. The heat balance equation using the adjusted net heat fluxes becomes:

$$V_i \frac{dT_i}{dt} = \sum_j Q_{ij} T_j + \sum_j E'_{ij}(T_j - T_L) + \frac{J_i V_i}{\rho C_p H_i} \qquad (8)$$

where:

H_i is the average depth of segment i. (cm)

Calibration

The methodology outlined above is used to determine the degree of horizontal and vertical transport necessary to match observed concentration gradients in the lake. Figure 12 shows the results of this analysis for vertical transport. The temerature gradients between the northern and southern Lake Huron epilimnia and hypolimnia are matched fairly well using the computed segment specific heat fluxes (Table 3) and incorporating a vertical exchange coefficient of 10 m^2/day (107.6 ft^2/day) during periods of non-stratification. There is no vertical exchange in the model during periods of complete lake stratification. This seasonal trend is simulated with a temporally varying vertical exchange coefficient as shown on figure 12. Surface temperatures which are most sensitive to the vertical mixing are well reproduced using this vertical variation. Hypolimnion temperatures are overestimated in Northern Lake Huron segment but are well reproduced for Southern Lake Huron with the exception of the rather erratic late August value.

A circulating flow equivalent to 2.2 cm/sec across the northern and southern lake epilimnia is incorporated and is consistent with surface

TABLE 3. Heat Flux Input for Transport Verification

Time (days)	Lakewide Average Heat Flux (gm-cal/cm^2-day)	Segment Specific Heat Flux* (gm-cal/cm^2-day)		
		Segment 1	Segment 2	Segment 3
97.5	120.37	139.32	124.62	-159.28
127.5	336.77	371.02	317.97	21.07
142.5	510.81	545.06	492.01	195.11
157.5	553.65	612.35	482.60	327.95
172.5	444.03	502.73	372.98	218.33
187.5	298.92	327.22	277.22	87.62
202.5	211.36	239.66	189.66	0.06
217.5	86.38	136.93	19.78	-64.37
232.5	39.24	89.79	-27.36	-111.51
247.5	6.82	55.32	-65.68	-70.18
262.5	-7.71	40.79	-80.21	-84.71
277.5	-77.27	-30.17	-154.87	-91.52
292.5	-99.74	-52.64	-177.34	-113.99
307.5	-188.77	-157.77	-238.27	-214.27
322.5	-234.09	-203.09	-283.59	-259.59
337.5	-406.57	-404.57	-421.07	-329.57
355.0	-815.50	-813.75	-830.25	-738.75

* K = 50 cal/cm^2-day-°C

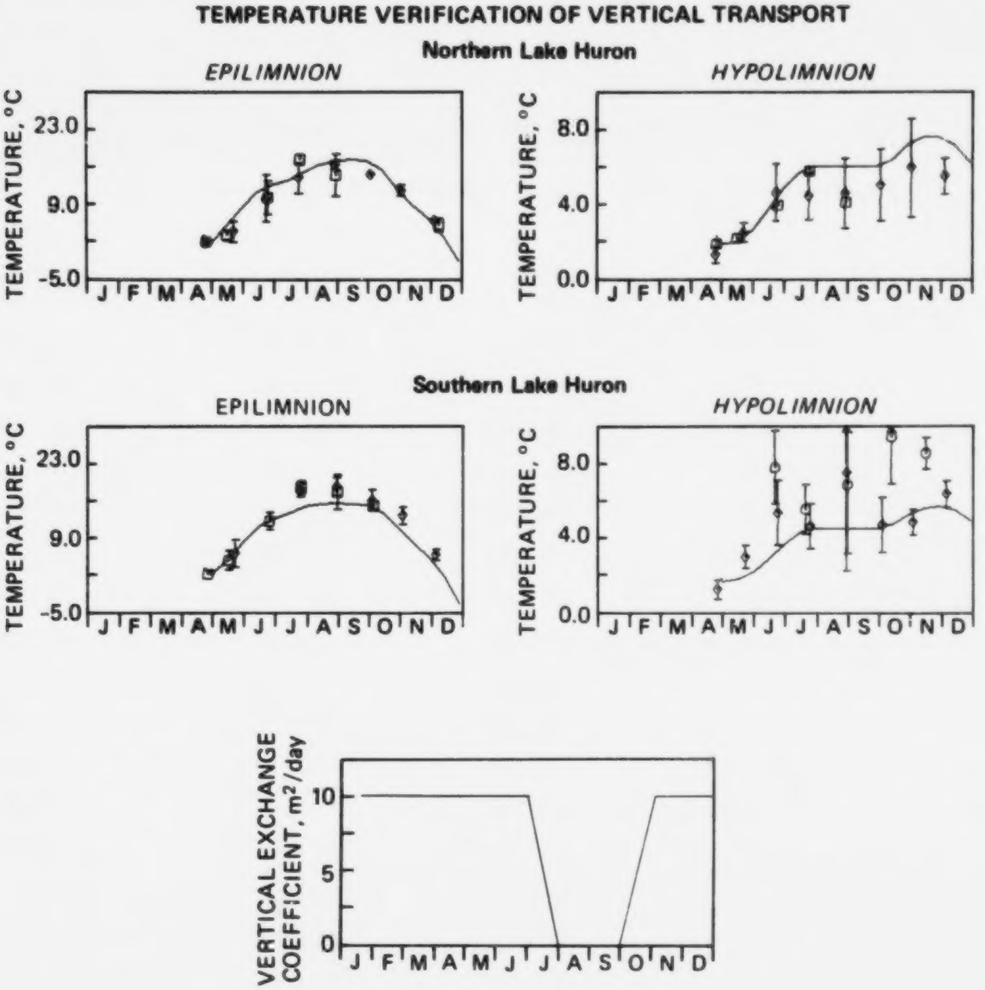


Figure 12. Vertical Transport Calibration

current magnitudes given by Ayers, et al. [16]. The horizontal exchange between the respective epilimnia and hypolimnia of northern and southern Lake Huron is set at 900 cm^2/sec based on estimates of horizontal diffusivities by Csanady [21]. Unfortunately there are no strong horizontal gradients here with which to calibrate these exchanges.

Figure 13 shows the horizontal transport calibration for exchange between Saginaw Bay and southern Lake Huron. The marked gradients for chlorides, temperature, and total phosphorus can be used to obtain consistent mass transport coefficients which give a consistent agreement between observation and calculation. The temperature calculation which is begun after the ice has melted is quite sensitive to the magnitude and timing of the exchange coefficient since Saginaw Bay is shallow and the heat flux markedly affects the computed temperature profiles. This is balanced by the loss of heat via the exchange flow.

Other estimates of the exchange flow are available, in addition to the Saginaw River advective flow which is inputted as a time-varying flow between 11,235 cfs (318 m^3/sec) and 1,561 cfs (44 m^3/sec) in order to reproduce the seasonal trend shown previously on fig. 2. The counterclockwise circulating flow from Lake Huron to Saginaw Bay is the major mechanism of this exchange. Danek and Saylor]22] have estimated a typical exchange rate between the inner and outer bay of 3700 m^3/sec (130,647 cfs) based on current meter and Lagrangian measurement during 1974. The Upper Lakes Reference Group [23] approximates the annual average exchange from the inner to the outer bay at 800 m^3/sec, and from the entire bay to Lake Huron at 5,000 m^3/sec. Richardson [24], using a sixteen segment model of Saginaw Bay, matched 1974 chloride profiles using an advective transport across inner and outer bay segment interfaces of 304-686 m^3/sec (10,737 - 24,229 cfs) during a thermal bar period and 1370 - 1750 m^3/sec (48,388 - 61,810 cfs) for the remainder of the year. The magnitude of the counterclockwise circulation from Lake Huron to Saginaw Bay for this calibration ranges from an equivalent of 425 m^3/sec (15,000 cfs) to 1,133 m^3/sec (40,000 cfs) with this exchange flow increasing in the spring and continuing through the summer as shown on fig. 13. Although there are differences in the magnitudes of the exchange rates estimated by various workers, the agreement shown on fig. 13 for three independent tracers indicates that the values used herein are consistent with observations.

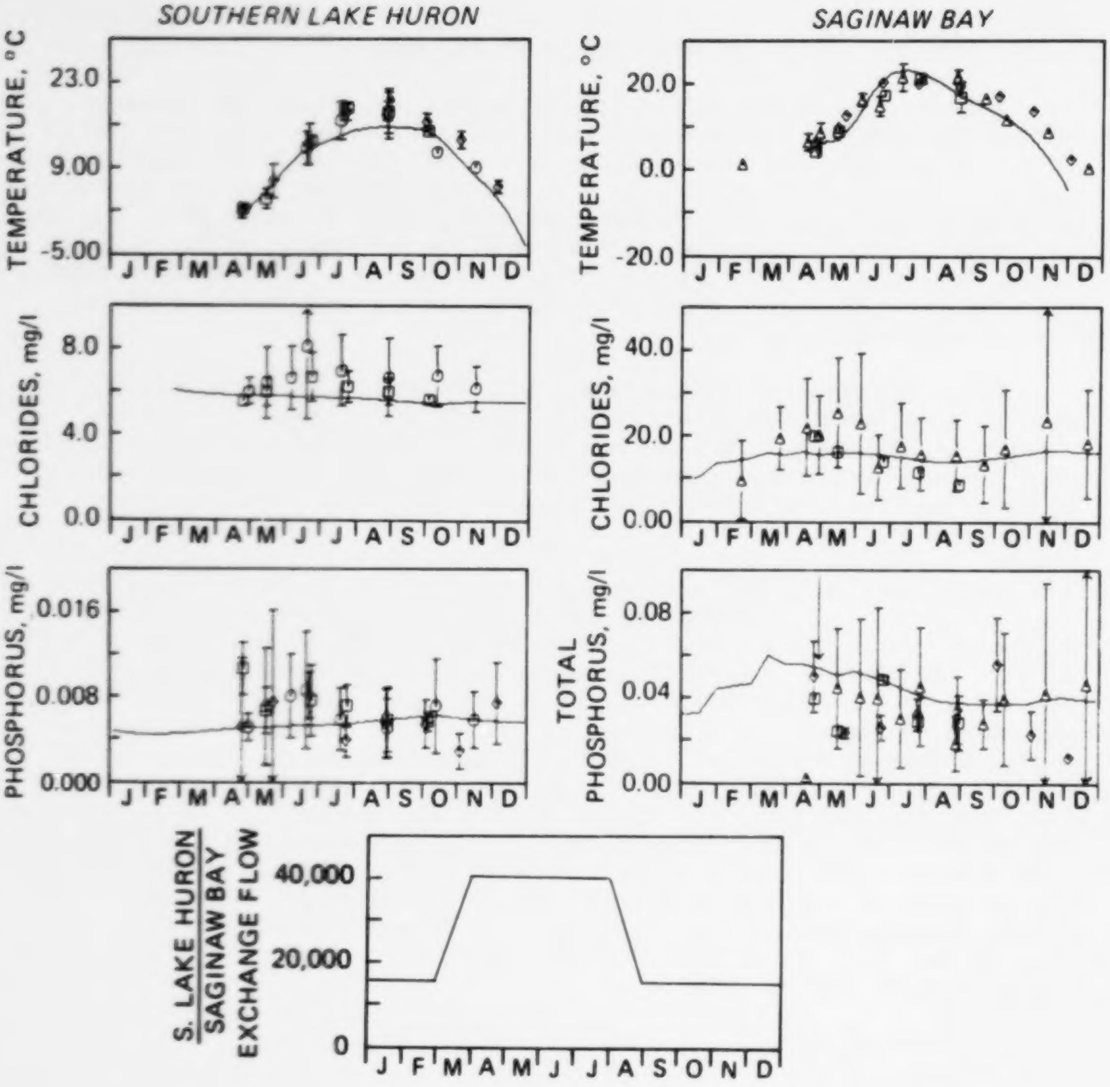


Figure 13. Horizontal Transport Calibration

SECTION 6

KINETICS

The interactions between the biological, chemical, and physical variables of concern must be specified in a way consistent with the conservation of mass equations that are the basis of this analysis. The transport components of these equations have been estimated in the previous section. The method to be used in this section, which is derived from physical chemistry, seeks to specify the rates of change of reacting species in terms of their concentrations. The application of these equations to essentially biological reactions has a long history [25] and is, in fact, currently a very active and fruitful guide for designing investigations and analyzing the resulting data.

The principle concern in the analysis of eutrophication phenomena is the growth and death of photosynthetic microorganisms. The framework for their kinetic equations derives from the work of Monod and it is this formulation which forms the basis of the work to be discussed subsequently.

GROWTH AND DEATH RATES

The fundamental kinetic equation for microorganisms in terms of their biomass, X, expresses their rate of growth as a function of a growth rate, μ, and a death rate, b:

$$\frac{dX}{dt} = \mu X - bX \tag{9}$$

The growth rate is a function of nutrient concentration and, for photosynthetic organisms, light intensity, and both μ and b are affected by temperature. In laboratory reactors the death rate is normally due only to endogenous respiration, the maintenance energy reaction necessary to keep the cell functioning, while in the natural settings predation by higher order organisms can substantially increase it, as shown subsequently.

Consider, first, the simplest situation with μ and b constant, that is there are abundant nutrients and the temperature and light intensity are constants. The solution to the kinetic equation is

$$X(t) = X(o)\, e^{(\mu - b)t} \tag{10}$$

and exponential growth or decay of microorganism biomass is predicted. In fact, such behavior is commonly observed in both laboratory reactors and natural waters. Examples of sustained exponential growth for the Lake Ontario and Lake Erie phytoplankton populations have been documented and analyzed [26]. However, other modes of population behavior are possible since the growth and death rates are not always constants but can vary substantially due to temperature, light, nutrient, and predation effects.

Temperature Dependence of Reaction Rate Constants

The temperature at which a reaction occurs has a significant influence on the reaction rate. This is true whether the reaction is simple (ideal gas) or a complex chain of biological reactions. For the case of chemical reactions at equilibrium it is known from thermodynamics that the equilibrium constant, K_{eq}, has an exponential temperature dependence. The usual formula is:

$$\frac{d \ln K_{eq}}{dT} = \frac{\Delta H_r^o}{RT^2} \tag{11}$$

which upon integration and assuming that ΔH_r^o, the enthalpy change of the reaction, is constant, yields,

$$K_{eq} = K' e^{-\frac{\Delta H_r^o}{RT}} \tag{12}$$

where K' is the integration constant, R is the universal gas constant and T is the absolute temperature. For the rate constants, k, Arrhenius proposed the analogous relationship

$$\frac{d \ln k}{dT} = - \frac{E}{RT^2} \tag{13}$$

which leads to an exponential temperature variation. E is called the activation energy of the reaction.

Since the absolute temperature scale is somewhat inconvenient, the Arrhenius temperature variation equation can be recast in a more useful form. If

$$k(T) = k' e^{-E/RT} \tag{14}$$

and $T = T_{20} + (T_c - 20.)$ where T_c is temperature in centigrade and $T_{20} = 293.16^oK$ then Eq. (14) becomes:

$$k(T) = k_{20}\ \theta^{(T_c-20)} \tag{15}$$

with

$$k_{20} = k' e^{-E/RT_{20}} \tag{16}$$

$$\theta = e^{+E/RT_{20}^2} \tag{17}$$

where the approximation $(1 + \varepsilon)^{-1} \simeq 1 - \varepsilon$ for $\varepsilon << 1$ has been used. The normal range of θ for chemical and biological reactions, over the range of interest (5° - 35°C) is 1.01 to 1.15, corresponding to an activation energy of 1.7 to 24 kcal/mole.

The temperature dependence of biological reactions is often reported in terms of Q_{10}, the ratio of the reaction rate at 20°C to that at 10°C. It is clear from the definition of θ that $Q_{10} = \theta^{10}$. Thus a $Q_{10} = 2$ implies that $\theta = 1.072$, a common value for biological reactions.

The exponential temperature dependence of algal growth and respiration rates is clearly seen in fig. 14, a plot of log μ and log b versus T. The sources of this data have been presented previously [27]. A detailed study of marine phytoplankton growth rate temperature dependence has been presented by Eppley [28] which indicates that the maximum growth rates vary with θ = 1.065.

It is well known, however, that a continually increasing growth rate with temperature is not realistic and, as higher temperatures are reached, the growth rate abruptly stops increasing and begins decreasing usually more sharply than it increased [29]. This effect can be important if species-specific calculations are being made. However for biomass as the dependent variable, the growth rate of an aggregration of species continues to rise until a maximum is reached at which no species can function. This is clearly shown in Eppley's fig. 7 [28] for which there exist species that can grow at maximal rates to beyond 25°C. Since the maximum temperatures reached in Saginaw Bay do not exceed this value, the decrease in growth rate due to high temperatures is not included in this calculation.

Light Dependence

For photosynthetic organisms, a relationship between growth rate and incident light energy is to be expected and this dependency has been studied quite intensively. However, until recently it is not growth rate that has been measured but primary production: the rate at which either O_2 is evolved, or CO_2 is assimilated. If the carbon synthesis reaction of algae is taken as equivalent to growth, which is correct for carbon as the measure of biomass, then the primary production rate is a measure of the growth rate. This assumption can be inaccurate for short term experiments, especially if environmental conditions are markedly varied during the measurement or for different measures of biomass. However, it provides a convenient starting point for the analysis.

Let $P(I)$ be the rate of primary production and P_m be the observed maximum rate of primary production at high light intensity. Further assume that the biomass of the population is constant throughout the measurements as light intensity varies. For this situation a number of expressions have

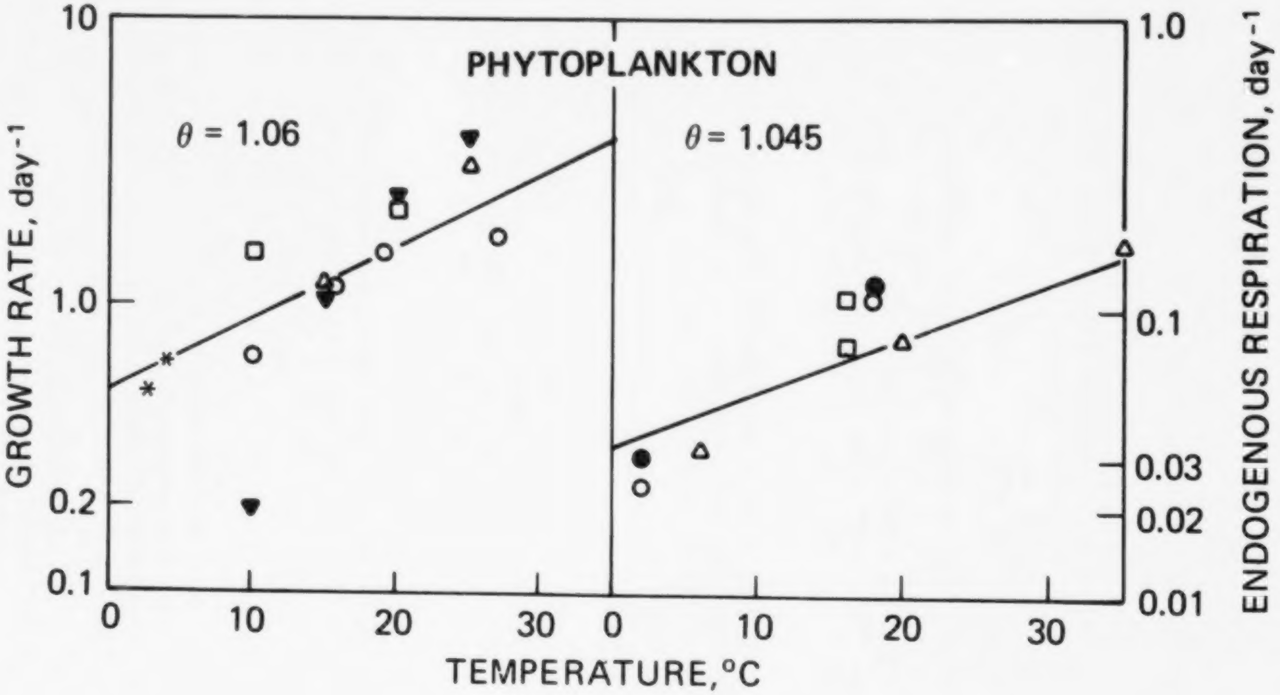


Figure 14. Exponential dependence of growth rate and respiration rate as a function of temperature. Data are from [27]. Straight lines correspond to the values of θ as indicated.

been proposed that relate $P(I)/P_m$ to light intensity. The original suggestion by Talling [30] is:

$$P(I) = P_m \frac{(I/I_k)}{\sqrt{1 + (I/I_k)^2}} \qquad (18)$$

where I_k is related to the slope of the photosynthesis-light relationship low intensities:

$$\frac{1}{I_k} = \frac{1}{P_m}\left(\frac{dP}{dI}\right)_{I=o} \qquad (19)$$

This expression predicts a continuously increasing rate as intensity increases. However, it has been observed that at higher intensities the rate decreases. An expression with this property, proposed by Steele [31] is;

$$\frac{P(I)}{P_{max}} = \frac{I}{I_s} e^{-\frac{I}{I_s} + 1} \qquad (20)$$

which reaches a maximum at $I = I_s$. As has been shown [27], this behavior is observed and the shapes are comparable to eq. (20). The relationship between I_k and I_s is easily found from eq. (19), namely $I_s = e\ I_k$. Although these expressions are somewhat different, it happens that for applications where depth-averaged primary production is required, they produce nearly equivalent expressions.

The light intensity in a body of water usually changes with depth as an exponentially decreasing function of depth. Thus

$$I(z) = I_o\ e^{-K_e z} \qquad (21)$$

For a particular volume segment of depth, H, for which the biomass is uniformly distributed in depth the average primary production and, by inference, the average growth rate is calculated from the expression:

$$\frac{P_{av}}{P_m} = r = \frac{f}{H} \int_o^H P[I(z)]dz \qquad (22)$$

where f is the fraction of daylight, the photoperiod, and r is the reduction factor due to the non-optimal light distribution. But from eq. (21):

$$dz = - dI/K_e I \qquad (23)$$

so that;

$$r = \frac{f}{K_e H} \int_{I(H)}^{I(o)} \frac{P(I)dI}{I} \qquad (24)$$

The evaluation of this integral is straightforward for both expressions of P(I). For eq. (18), the average yields:

$$r = \frac{f}{K_e H} \ln \left[\frac{\iota_o + \sqrt{1+\iota_o^2}}{\iota_H + \sqrt{1+\iota_H^2}} \right] \qquad (25)$$

where $\iota_o = I(o)/I_k$ and $\iota_o = I(H)/I_k$. For eq. (20), the average yields:

$$r = \frac{ef}{K_e H} \left[e^{-\alpha_H} - e^{-\alpha_o} \right] \qquad (26)$$

where $\alpha_o = I(o)/I_s$ and $\alpha_H = I(H)/I_s$. A direct comparison is possible since $I_s = e\, I_k$. For depths at which α_H and $\iota_H \rightarrow 0$ the comparison is shown below where $f/K_eH = 1$ for convenience of presentation:

I_o/I_s	Talling Eq. (25)	Steele Eq. (26)
3.0	2.80	2.58
2.0	2.39	2.35
1.0	1.73	1.72
0.5	1.11	1.07
0.25	0.64	0.60

The differences are quite small with the effect of decreasing primary production in Steele's eq. (20) amounting to less than 10% for the highest incident intensity.

It is also interesting to note that for either expression the difference between normalized surface intensities of 3.0 and 2.0 is small indicating that changes in I_s when the surface intensity is large have only a small effect. However the converse is true for small I_o/I_s where the reduction is almost proportional. This is confirmed in section 9 which illustrates the sensitivity of the solution to I_s. In practice the measured incident solar radiation is the total daily flux: I_{av}. Since this includes the dark period as well, the mean daily radiation intensity is $I(o) = I_{av}/f$. This is the quantity used in evaluating the light reduction factor (see Table A1).

Nutrient Dependence

The nature of the dependence of phytoplankton growth rate on nutrient concentration is a topic for which a large body of experimental information exists. For this investigation the principle nutrients of concern for Lake Huron and Saginaw Bay are inorganic phosphorus and nitrogen. Recent investigations of the growth kinetics of single species in chemostats have concentrated on the dependence of growth rate, μ, as a function of internal cellular concentrations, q, of phosphorus [32] and nitrogen [33].

For investigations of single nutrient limitation of algal growth, the following expression has been found to apply to observed growth rate μ [34]:

$$\frac{\mu}{\mu'_m} = 1 - \frac{q_o}{q} \tag{27}$$

where μ'_m is the theoretical maximum growth rate at infinite cell quota, q is the internal cell quota in units of mass of nutrient per cell, and q_o is the minimum cell quota for that nutrient. Thus the growth rate is a saturating function of the internal "available" nutrient concentration $q - q_o$. The external concentration, S, together with the internal concentration, determines the cellular uptake rate of the nutrient, v. For a specific internal concentration the relationship of uptake to external concentration is found to be:

$$v = \frac{V_m S}{K_m + S} \tag{28}$$

a Michaelis-Menton function with half saturation constant K_m.

In order to examine the implications of these equations, consider the situation that occurs at steady state. For this situation an equilibrium is established between the internal cell quota and cell growth so that:

$$v = \mu q \tag{29}$$

and nutrients are assimilated only insofar as they are required for cell growth. For this case, it is possible to express cell growth rate as a function of external nutrient concentration [34]. Using eqs. (27), (28), and (29) to solve for q yields:

$$\mu = \frac{\mu_m S}{K_s + S} \tag{30}$$

where

$$\mu_m = \frac{\mu'_m}{1 + \dfrac{\mu'_m q_o}{V_m}} \tag{31}$$

$$K_s = \frac{\mu'_m q_o K_m}{V_m\left(1 + \frac{\mu'_m q_o}{V_m}\right)} \qquad (32)$$

Thus if these parameters are in fact constant, the Monod theory applies. However, it has been found that V_m varies inversely with q, i.e. more rapid nutrient assimilation occurs for small internal cell quota, and, therefore, the behavior is more complex than a purely Michaelis-Menton expression. For example, for phosphate limited Scenedesmus, the uptake velocity is found to be [37]

$$V = \frac{V_m S}{K_m + S} \cdot \frac{K_i}{K_i + i} \qquad (33)$$

where i is the internal nutrient concentration of total inorganic polyphosphate and K_i is a half saturation constant for this dependency.

For this type of behavior the relationship of growth to external nutrient concentration is no longer exactly given by eq. (30). However, if K_s is defined appropriately, the differences are of no practical importance [36] and eq. (30) applies as a very good approximation. This is illustrated in fig. 15 which compares eq. (30) to that which results from using the cellular nutrient expression for growth, eq. (27); the cellular and external nutrient equation for uptake, eq. (33) with $i = q - q_o$; and assuming cellular equilibrium, eq. (29). The difference is of no practical importance.

However, the Monod behavior occurs only if eq. (29) holds, which essentially specifies that there is no dynamic luxury uptake. Rather the uptake of nutrients is occurring in quantities sufficient to meet the cell quota at that growth rate. Thus depending on the conditions of the experiments or in the prototype, Monod's theory may apply only approximately, and only for conditions approaching equilibrium for the internal cell quota. An estimate of the time scale for this condition to be reached, based on a dynamic perturbation analysis [36], indicates that it is at least $1/4\ \mu_m$ where μ_m is the non-nutrient limited growth rate of the population. Thus, except for short-term laboratory growth rate experiments, it is expected that cellular equilibrium is a reasonable approximation.

The major difficulty with Monod's theory of microorganism growth as applied to phytoplankton is that the variation of cell stoichiometry is not taken into account in the uptake expressions for nutrients. The problem is compounded by the lack of a clear choice of the proper biomass or aggregated population variable for a natural assembledge of plankton [36]. From a practical point of view the population variable for which a sufficient quantity of data exists for the Great Lakes is chlorophyll-a and the appropriate stoichiometry is the nitrogen and phosphorus to chlorophyll-a ratios. It is well known that these ratios vary considerably with external nutrient concentration and past population history. Large ratios correspond to excess

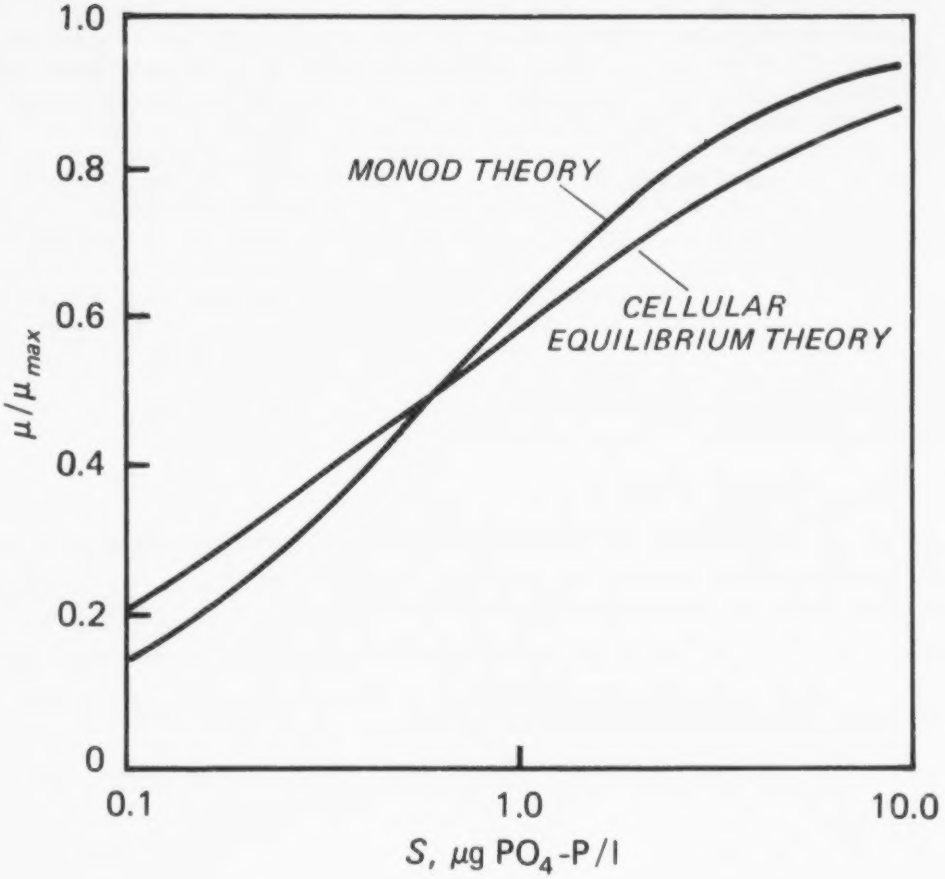


Figure 15. Ratio of growth rate to maximum growth rate vs. external phosphorus concentration for external phosphorus concentration for Scenedesmus sp. (37). m'm = 1.33 day^{-1}; qo = 1.6 f-mol/cell; V_m = 4.8 f-mol/cell/hr; K_m = 18.6 μg PO_4 - P/ℓ; K_i = 0.73 f-mol/cell. (f-mol = 10^{-1} 5 mol PO_4-P).

nutrients and small ratios correspond to that nutrient limiting the growth rate. Thus the choice of the relevant ratio can be made with the situation of interest in mind. Since the population to be discussed subsequently is primarily phosphorus limited, the stoichiometry chosen can reflect these facts. The operational consequences of this choice is that the population stoichiometry under non-limiting conditions will be underestimated but the maximum chlorophyll concentrations under limiting conditions should be correctly estimated. Hence there is a tradeoff between a probable lack of realism during a portion of the year versus a correct estimate of population chlorophyll during the period of nutrient limitation. Since this is usually the critical period, and most questions to be answered are usually sensitive to the maximum population size, this choice is a practical expedient.

A more detailed discussion of these issues, together with tabulations of the experimentally determined ratios is given elsewhere [37]. What is important to realize is that the kinetics which finally emerge are essentially empirical since they are applied to natural populations with chlorophyll as the aggregated population variable whereas their basis is derived from single species experiments.

APPLICATION TO BATCH KINETICS

Let P be the phytoplankton chlorophyll concentration and a_{NP}, a_{pP}, etc. be the stoichiometric ratios of nitrogen, N, and phosphorus, p, to chlorophyll. The rate of assimilation of inorganic nitrogen is then $a_{NP} G_P P$ where G_P is the population growth rate and $G_P P$ is the rate of increase of population chlorophyll. The assimilation rate of phosphorus is $a_{pP} G_P P$, and so on for all the constituents of the population.

The kinetic equations which result from these considerations are:

$$\frac{dP}{dt} = (G_P - D_P)P \qquad (34a)$$

$$\frac{dN}{dt} = -a_{NP} G_P P \qquad (34b)$$

$$\frac{dp}{dt} = -a_{pP} G_P P \qquad (34c)$$

$$\frac{ds}{dt} = -a_{SiP} G_P P \qquad (34d)$$

where D_P is the endogenous respiration rate, Si is the dissolved silica concentration and a_{SiP} is the silica to chlorophyllstoichiometric ratio of the population. For this application to batch kinetics recycle has been neglected. As shown subsequently it is of prime importance for the actual situation in the Great Lakes.

An application of these equations has been made for a series of batch phytoplankton growth experiments using a natural assemblage of phytoplankton from the estuary of San Francisco Bay [38]. This population is exclusively nitrogen limited. The calculation of the maximum growth rate for the population rate is based on the temperature and light intensity used for the experiments. As shown previously, the effect of temperature on algal growth and respiration is well represented by an exponential relationship below the optimum temperature. The effect of a non-optimal light intensity is to reduce this growth rate from its maximum. If it is assumed that these effects are multiplicative, it follows that:

$$G_P = K_1\theta_1^{T-20} \cdot \frac{I}{I_s}e^{-(\frac{I}{I_s}+1)} \frac{N}{K_{sN}+N} \cdot \frac{p}{K_{sp}+p} \tag{35}$$

and that:

$$D_p = K_2\theta_2^{T-20} \tag{36}$$

Note that the depth-averaged form of the light reduction equation is not used since the reaction vessel is completely illuminated.

A control and two different initial conditions for the nutrients, 0.2 mgN/ℓ and 0.5 mgN/ℓ were examined. The results for these experiments together with the calculations are presented in fig. 16. It is clear that the limiting nutrient is inorgan nitrogen since its concentration is calculated to decrease to below the half saturation constant, K_{sN}, as the algae grow to their peak. The behavior of the phytoplankton biomass and nitrate nitrogen are well represented by the calculations. The uptake of dissolved silica is less well represented and the silica to chlorophyll ratio represents a compromise for the observations. The uptake of phosphate is not in agreement with the observations. The phosphorus continues to decrease beyond that required for the growth, as indicated by the decrease of both algae and inorganic phosphorus during the later portion of the experiment. This luxury uptake cannot be explained in the terms of the Monod theory and constant stoichiometric coefficients, and, as pointed out previously, the variation of the stoichiometry of the microorganisms during short term experiments is perhaps the most frequently encountered effect which violates the assumptions of the Monod theory. Nevertheless the predicted behavior with respect to the limiting nutrient is reasonable and supports the use of these kinetics for calculation of changes in chlorophyll as a function of nutrient concentrations.

ZOOPLANKTON KINETICS

A major factor in the reduction of phytoplankton biomass after the spring bloom in the Great Lakes is the predation pressure exerted by the herbivorous zooplankton. In order to quantify this effect and relate it to the magnitude of the phytoplankton and zooplankton populations present it is necessary to develop an additional set of kinetic relationships. The basis for these equations are not the substrate-microorganism formulations applicable to dissolved nutrients and bacteria or algae but rather the relationships that have been developed to describe the behavior of larger predatory organisms such as fish. The principle difference is the mode of feeding.

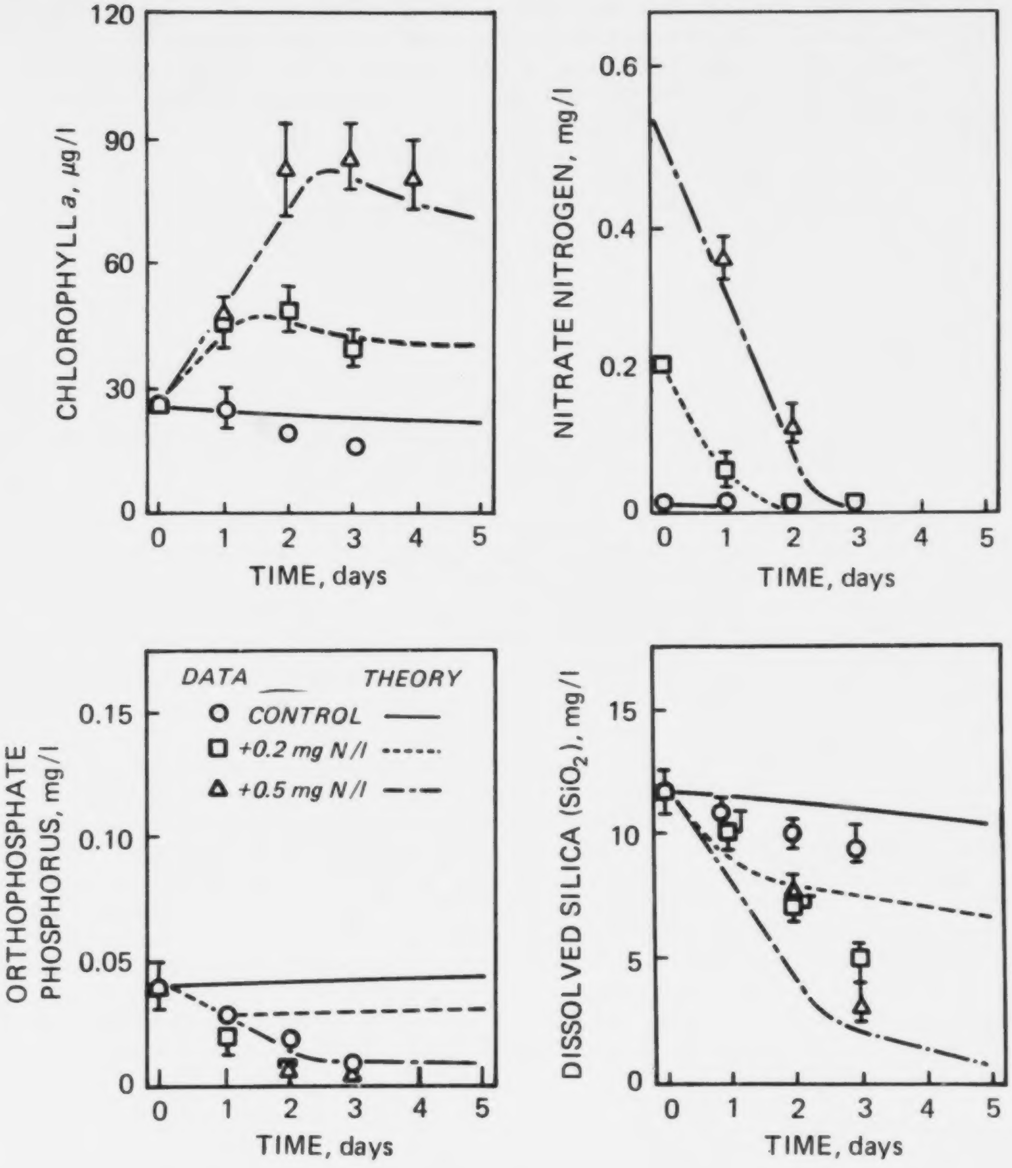


Figure 16. Application of algal growth and nutrient uptake equations (34) to batch kinetic data

Phytoplankton are the prey and the predators are the herbivorous and omnivorous zooplankton. The classical equations of predator-prey interaction are those of Volterra [25] which, for phytoplankton-herbivorous zooplankton interactions, take the form:

$$\frac{dZ_1}{dt} = (G_{Z1} - D_{Z1})Z_1 \tag{37}$$

with the growth rate G_{Z1}, given by:

$$G_{Z1} = a_{CP}\,\varepsilon\, C_g\, P \tag{38}$$

where Z_1 is the herbivorous zooplankton biomass, a_{CP} is the zooplankton/phytoplankton stoichiometric ratio which, as in this case with zooplankton biomass in carbon units, corresponds to the carbon/chlorophyll ratio of the phytoplankton. The interaction coefficient $\varepsilon\, C_g$ can be thought of as a specific filtering rate C_g, with units ℓ/mg C-day corresponding to the specific (i.e. per unit biomass) filtering rate of the zooplankton population, and ε, the assimilation efficiency. For raptorial feeding these interpretations do not apply and the coefficient must be regarded as empirical. The loss rate, D_{Z1}, is due to both respiration and higher order predation.

Growth Rate

The filtering rate defined above varies as a function of the concentration of the prey, the size of the grazing organism, and the temperature [39]. These effects are quite significant and are taken into account using the available data to suggest functional forms and the range of the parameters that are reasonable.

To relate these terms to the more classical analysis of zooplankton feeding and growth, consider the ration, R, the weight of food consumed per animal per unit time. Investigations of the feeding of crustacean zooplankton indicate that the relationship of the ration to increasing food concentration is to increase in proportion to the increasing but small food concentrations but then to level off and reach a maximum, R_m, as food concentration continues to increase. This type of behavior, observed in the feeding behavior of fish by Ivlev, can be described by the equations [39,40,41]:

$$R = R_m\,(1 - e^{-\xi P}) \tag{39}$$

In terms of the growth equation (38), this suggests that the filtering rate is decreasing as the food concentration increases. If a hyperbolic function is used to represent this behavior as done previously [29], then the ration changes as

$$R = \frac{C'_{gm} \; P \; K_{mg}}{K_{mg} + P} \tag{40}$$

where C'_{gm} is the maximum filtering rate (ℓ/animal-day) and K_{mg} is the half saturation constant for filtering. By matching the maximums and the initial slopes of these two expressions the relationships:

$$K_{mg} = \frac{1}{\xi} \tag{41}$$

$$C'_{gm} = \xi R_m \tag{42}$$

are derived. Table 4, adopted from Sushchenya [39] illustrates some representative values. The value of the half saturation constant varies widely with lower values in the range of 1-10 μg Chl-a/ℓ and appears to depend strongly on the species of both phytoplankton and zooplankton involved.

The hyperbolic dependence of the specific filtering rate on phytoplankton concentration is illustrated in Fig. 17. The data from Richman [42] for Diaptomus oregonensis feeding on Chlamydomonas and Chlorella is well represented by eq. (40) with K_{mg} = 40,000 cells/ml corresponding to an estimated K_{mg} = 8 mg wet. wt./ℓ (11-32 μg Chl-a/ℓ).

The relationship of the ration to body weight of the animal follows an equation of the form:

$$R = \alpha \, W^{\beta} \tag{43}$$

at constant food concentration and temperature. A review of the available values for β indicates that it varies from a low of $\beta \simeq 0.6$ to a high of $\beta \simeq 0.9$ with the higher values predominating [41]. This suggests that the ration, defined per unit zooplankton biomass, R/W, is less dependent on the absolute body weights of the population since:

$$\frac{R}{W} = \alpha \, W^{\beta-1} \tag{44}$$

and 1-β is in the range of 0.1 to 0.4. For a 10 fold increase in W, the predicted change in R is a factor of 3 to 8 increase whereas the change in R/W is only a 21 to 60% decrease. Thus for a formulation that aggregates the zooplankton population into a biomass concentration, the specific ration R/W is the useful parameter, since it is closer to being constant with changes in body weight. This useful fact gives some support to the validity of aggregating the zooplankton in terms of biomass rather than as individuals, a procedure which is, as with the phytoplankton, a practical expedient Specific filtering rates have been summarized [27] and vary in the range 0.1 - 4.0 ℓ/mgC/day with the majority of the rates in the vicinity of 1-2 ℓ/mgC/day.

TABLE 4. GRAZING CONSTANTS [39]

Species Zooplankton	Phytoplankton	R_m $\frac{\text{mg wet wt.}}{\text{animal/day}}$	ξ $\frac{\ell}{\text{mg wet wt.}}$	C'_{gm} $\frac{\text{m}\ell}{\text{animal/day}}$	K_{mg} $\frac{\text{mg wet wt.}}{\ell}$	$K^{\#}_{mg}$ $\frac{\mu\text{g Chl-a}}{\ell}$
Daphnia longispina	Various Algae	0.0325	0.457	14.9	2.18	2.9-8.7
Daphnia pulex	Chlamydomonas	0.0525	0.310	16.3	3.23	4.3-13.0
Acartia clausi	Various Algae	0.0011	1.19	1.31	0.841	1.1-3.4
Diaphanosoma brachyurum	Chlorella	0.00575	1.04	6.00	0.958	1.3-3.8
Artemia Salina	Dunaliella	2.15	0.0051	10.89	197.	260-780
Bosmina longirostris	Chlorella	0.21§	0.008§	3.87	49	65-200
Simocephalus vetulus	Chlorella	0.36§	0.012§	9.53	38	50-150
Eurytemora hirundoides	Nitzschia	0.13†	0.00052†	0.16	830	-
Neomysis vulgaris	Nitzschia	13.8†	0.00075†	24	580	-

Estimate using 10% wet wt. = carbon wt. and C/Chl-a = 25-75

§ Assuming Chlorella wet wt. = 200 μμg [45]

† Assuming Nitzschia wet wt. = 240 μμg [45]

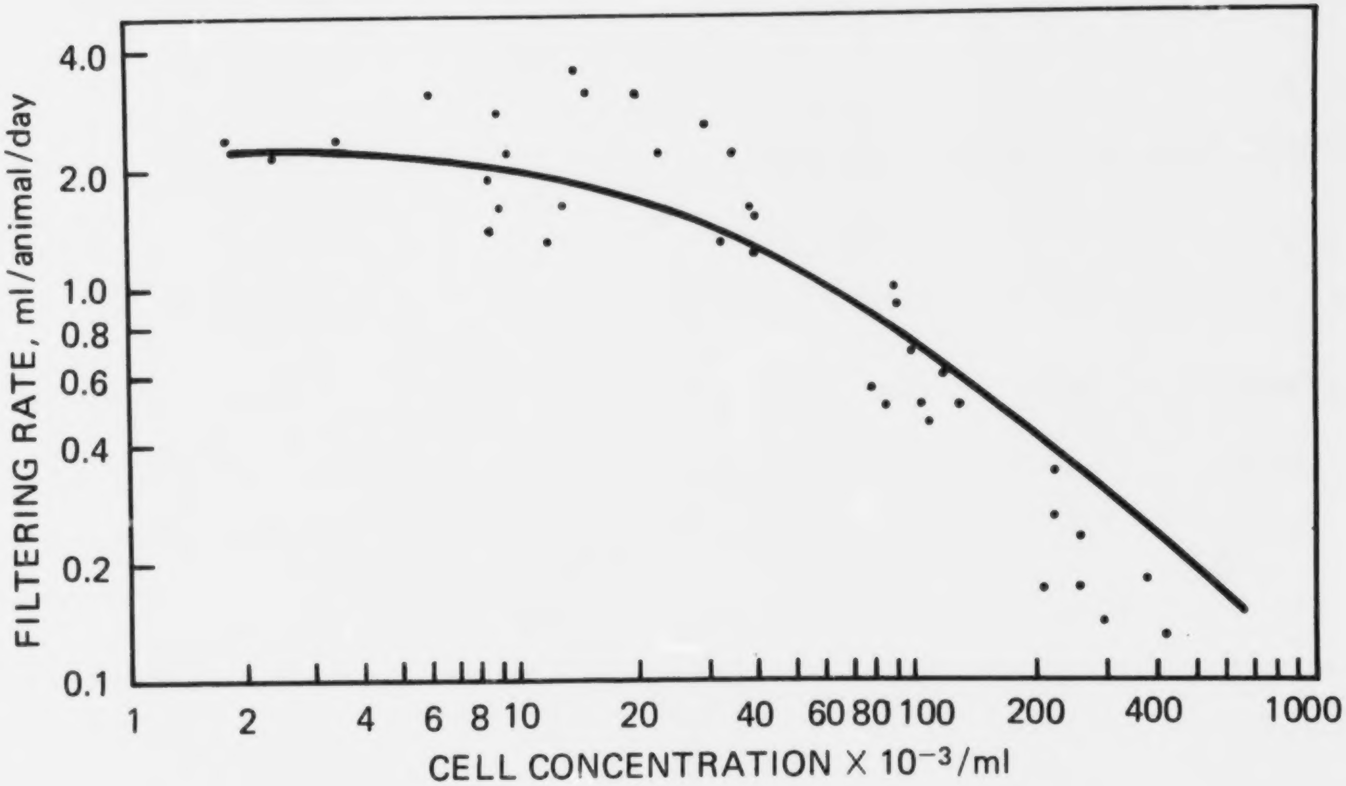


Figure 17. The relationship between filtering rate of Diaptomus oregenensis and prey concentration (chlamydamonus and chlorella). C'_{gm} = 20 mℓ/animal/day; K_{mg} = 40,000 cells/mℓ. Curve is equation (40).

The temperature dependence of the filtering rate has been summarized [27] and the results indicate that, in contrast to all other biological rates included in the kinetics, the dependence is linear with temperature, with a zero filtering rate at 0°C a reasonable simplification. Thus the specific filtering rate is specified at 20°C and multiplied by T/20°C to account for its temperature dependence.

The assimilation efficiency, ε, has been reported in the range of 40-90% [44]. The efficiency is the fraction of the food ingested which is not excreted but is used for growth and metabolism. It has been observed to decrease with increasing ration [39] and increasing food concentration [43]. Since ration increases with food concentration it seems reasonable to incorporate this effect as dependent on food concentration using a hyperbolic relationship of the form: $\varepsilon = \varepsilon_m K_{m\varepsilon}/(K_{m\varepsilon} + P)$ by analogy to the grazing dependence with $K_{m\varepsilon}$ as the half saturation constant.

The result of the above considerations is that the growth rate of the herbivorous zooplankton, G_Z, grazing on phytoplankton at concentration P is of the form:

$$G_Z = a_{CP}\ \varepsilon(P)\ C_g(P,T)P \tag{45}$$

where

$$\varepsilon(P) = \frac{\varepsilon_m K_{m\varepsilon}}{K_{m\varepsilon} + P} \tag{46}$$

and

$$C_g(P,T) = C_{gm}\left(\frac{T}{20}\right)\frac{K_{mg}}{K_{mg} + P} \tag{47}$$

The parameters to be specified are the maximum grazing rate at 20°C, C_{gm}; the grazing half saturation concentration of phytoplankton, K_{mg}; the maximum assimilation efficiency, ε_m; and its half saturation constant, $K_{m\varepsilon}$; and the zooplankton to phytoplankton stoichiometric ratio, a_{CP}.

Death Rate

The components of the death rate included in this formulation of herbivorous zooplankton kinetics are the loss of biomass due to metabolism as measured by respiration, and that due to predation by carnivorous zooplankton.

The respiration rate of zooplankton as measured by their O_2 consumption has been found to be a strong function of both organism weight and temperature [45]. The dependency on organism weight is analogous to that found for grazing rates, eq. (43), with the exponent in the same range. Thus the specific respiration rate, the rate per unit biomass rather than per animal, can be expected to be more nearly constant with respect to organism weight although some variation has been found [41]. For organisms from temperate waters that rate varies from 4.6 to 2.3 $\mu\ell O_2$/mg dry wt./hr. for a 10 fold change (0.1-1.0 mg dry wt./animal) in organism weight.

The temperature variation of the respiration rate is an exponential function with θ found to be in the range of θ = 1.060 to 1.120 as shown in Fig. 18, a plot of the log of the ratio of specific respiration rate at T °C to that at 20°C. The legend, source, and references for these data have been given previously [27]. Thus respiration loss rate can be represented by the equation:

$$R_{Z1} = K_3 \ \theta_3^{T-20} \tag{48}$$

where R_{Z1}, the respiration rate in per day units, is available from the specific oxygen consumption rate if the fraction of the dry weight that is carbon and the respiratory quotient ($RQ = \Delta CO_2$ produced/ΔO_2 consumed) are known. For reasonable values of these ratios (40% C/dry wt. and RQ = 1) the observed rates are in the range 0.06 to 0.2 day^{-1} [41]. The observed values of the zooplankton respiration rate, K_3, are somewhat less than the equivalent phytoplankton respiration rates which is consistent with the observation that specific rates appear to decrease slightly with organism size or weight.

Other experimentally observed effects which have not been explicitly included in the kinetics is the possible existence of a phytoplankton concentration at which grazing ceases [46] and the effect of nocturnal grazing as opposed to continuous or daily average grazing [47]. Perhaps the rather large range in observed parameters for the present paramerization reflects these effects as well as the specifics of the grazing experiments themselves, e.g. short versus long term experiments and starved versus normal zooplankton.

The other major component of herbivorous zooplankton mortality is predation by the carnivorous zooplankton population. The importance of carnivorous grazing pressure in Lake Ontario is evident from the calculations of Thomann et al. [48]. An interesting example of this effect has been observed and quantified [49] for Daphnia grazing on phytoplankton, measured as chlorophyll, and being preyed upon by Leptodora. The relevant constants derived from the data are: $a_{CP} \ \varepsilon_m \ C_{gm} = 0.025$ $\ell/\mu gC$/day; zooplankton respiration rate = 0.088 day^{-1}; and Leptodora filtering rate of 9.5 $m\ell$/animal/day, all of which are within reported ranges for these parameters. The formulation of the carnivorous grazing adopted in this analysis is entirely classical [25] and corresponds to the Volterra predator-prey formulation without saturating effects. That is the death rate by predation takes the form $C_{g2}(T)Z_2$ where the grazing rate is linear in temperature and Z_2 is the carnivorous zooplankton biomass.

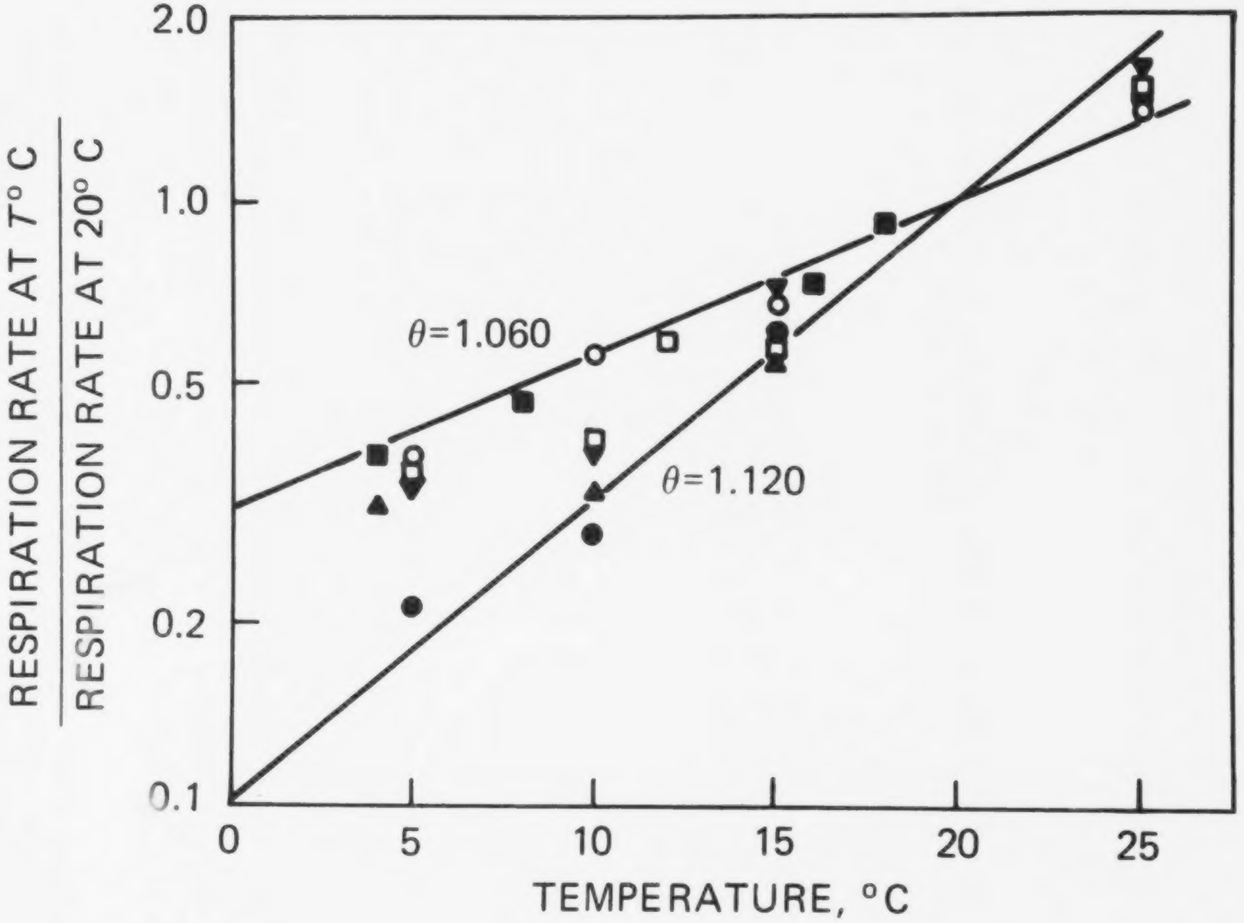


Figure 18. Logarithm of normalized zooplankton respiration rate as a function of temperature. Exponential temperature dependence in the range θ = 1.06 - 1.12 as indicated. For legend and references see [27].

The growth and death rates for the carnivors in turn determine their population size:

$$\frac{dZ_2}{dt} = (G_{Z2} - D_{Z2})Z_2 \qquad (49)$$

The growth rate follows from the filtering rate and an assimilation efficiency ε:

$$G_{Z2} = \varepsilon C_{g2}(T)Z_1 \qquad (50)$$

The death rate is the sum of respiration losses and an empirical constant, K_5, which accounts for higher order predation so that:

$$D_{Z2} = K_4 \theta_4^{T-20} + K_5 \qquad (51)$$

At this level of resolution Thomann et al. [48] have shown that, at least computationally, higher order dynamic predator-prey equations do not materially influence the dynamics of the lower members of the food chain on an annual cycle.

NUTRIENT RECYCLE

The recycling of nutrients, that is, the transformation from unavailable particulate and soluble organic forms to the available soluble inorganic forms, is the critical step in completing the cyclic nutrient pathways in aquatic systems. The purpose of this section is to present evidence that the rate of this recycle reaction for phosphorus in the lower Great Lakes is related to the size of the phytoplankton population. It is also shown that under simplifying assumptions the rate of recycle, together with the growth rate of the algae determines the fraction of the total phosphorus concentration which is present as either plankton, or in unavailable or available forms.

The importance of phosphorus recycle is well known. If no significant recycle occurred, the plankton would rapidly deplete the available form, and the unavailable form being generated by the algal metabolic losses and zooplankton excretion processes would build up and eventually account for all the phosphorus present, thus terminating the cycle. However since recycle does in fact occur, the balance between the three forms of nutrients is maintained.

The observational and experimental investigations of recycling have been described by a number of investigators [50,51]. The two major processes which contribute to the recycle are the predation by zooplankton and the metabolic losses of the algae and zooplankton themselves. The role of bacteria in the subsequent transformation has recently been documented [52].

Normally, healthy algal cells are not usually attacked by proteolytic bacteria but if the cells are deprived of essential nutrients and/or sufficient light the cells become permeable and soluble nutrients leak out. The phenomena can be quite rapid with up to 80% of the cell phosphorus and 20% of the cell nitrogen being released in 2-3 days [50]. The remainder of the cell nutrients are in the form of particulate cell fragments. The phenomena occurs as the population is stressed, possibly declining, and using its cellular constituents in its metabolism. In this report, the process is termed respiration, since it is most pronounced in dark conditions which characterize the oxygen consumption (e.g. the dark bottle of primary production studies) and nutrient release experiments that quantify the rates.

A nutrient release process also occurs during zooplankton grazing of algal populations. For example, during active feeding, Calanus retained 17% of the algal phosphorus for growth and excreted the remainder, 23% as fecal pellets and 60% as soluble phosphorus. For nitrogen 27% was retained while 38% was excreted as fecal pellets and 36% as soluble nitrogen [53]. A similar result for natural marine zooplankton populations has been observed where 60% of the total excreted phosphorus is in the form of phosphate [54]. Thus the result of algal respiration, mortality, and zooplankton grazing is to release nutrients in both soluble and particulate forms. A portion of the soluble nutrients are in the available form with the remainder present as organic compounds.

KINETIC FORMULATION

The detailed characterization of the forms of nutrients in natural waters: inorganic or organic, particulate or dissolved, requires extensive data that, at the low concentrations in Great Lakes waters, are difficult to obtain. Perhaps the most difficult differentiation is between detrital and phytoplankton-bound nutrient since no simple separation is possible. In order to characterize the recycle process and at the same time not complicate the formulation to the point of impracticality, it appears that the division of the nutrient into three forms: plankton-bound, available, and unavailable is a reasonable first step. The available phosphorus form is directly measured as soluble reactive phosphorus. A portion of the unavailable phosphorus is measured as dissolved organic phosphorus. The total phosphorus is also measured.

The formulation of the kinetics of recycle requires an equation which specifies the rate at which the unavailable nutrient is transformed to the available form. To be specific, let p_T, p_u and p_i be the concentrations of total, unavailable, and inorganic (= available) phosphorus respectively. The concentration of phosphorus associated with a concentration, P, of algal chlorophyll, is $a_{pP}P$ where a_{pP} is the phosphorus to chlorophyll ratio of the population. Similarly, if Z is the zooplankton carbon concentration, then $a_{pZ}Z$ is the zooplankton phosphorus.

Consider a situation in which transport and external sources can be neglected, i.e. a purely kinetic setting. The kinetic equations which describe phytoplankton and zooplankton growth and death, and phosphorus uptake and recycle, with the modification that a fraction $(1-\rho)$ of respired and excreted phosphorus is directly available, have the form [27,48]

$$\overset{\circ}{P} = (G_P - D_P - C_g Z)P \tag{52a}$$

$$\overset{\circ}{Z} = (G_Z - D_Z)Z \tag{52b}$$

$$\overset{\circ}{p}_u = \rho D_P P' + \rho(C_g ZP' - G_Z Z') + \rho D_Z Z' - Kp_u \tag{52c}$$

$$\overset{\circ}{p}_i = (1-\rho)D_P P' + (1-\rho)(C_g ZP' - G_Z Z') + (1-\rho)D_Z Z' - G_P P' + Kp_u \tag{52d}$$

where G_P, D_P are the epilimnion averaged growth and respiration rates for phytoplankton; G_Z, D_Z are the growth and death rates for zooplankton; C_g is the zooplankton grazing rate; ρ is the fraction of respired and excreted phosphorus that is in the unavailable form; $P' = a_{pP}P$ and $Z' = a_{pZ}Z$, the phosphorus equivalents of phytoplankton chlorophyll and zooplankton carbon; and K is the recycle rate of unavailable to available phosphorus, which is assumed to be first order with respect to p_u. In this notation total phosphorus is given by: $p_T = p_i + p_u + P' + Z'$. For steady state conditions the derivatives are all equal to zero and either eq. (52c) or eq. (52d) yields the following relationship:

$$\left(1 + \frac{K}{\rho G_P}\right) \frac{p_u}{p_T} + \frac{p_i}{p_T} + \frac{Z'}{p_T} = 1 \tag{53}$$

For the case that the fractions of the total phosphorus that are either in the available form, p_i/p_T, or bound as zooplankton biomass, Z'/p_T, are both small relative to one, eq. (53) simplifies to:

$$\frac{p_u}{p_T} \simeq \frac{1}{1 + \delta} \tag{54}$$

where:

$$\delta = \frac{K}{\rho G_P} \tag{55}$$

the dimensionless ratio of recycle rate to the growth rate - fraction unavailable product.

For rapid recycle relative to growth or for a small ρ, the unavailable fraction excreted or respired, $\delta >> 1$, and only a small portion of total phosphorus is in the unavailable form. Conversely for slow recycle relative to growth or a large unavailable excreted or respired fraction, $\delta < 1$, and most of the phosphorus is in the unavailable form. Thus the dimensionless parameter, δ, is the important characteristic of the kinetics which determines the distribution of total phosphorus for the case that the available and zooplankton fractions are small relative to the algal and unavailable fractions.

The magnitude of the recycle rates from various laboratory experiments are listed in Table 5. The range is 0.01 to 0.06 day^{-1} corresponding to half lives of approximately 12 to 70 days. The temperature coefficients are within the expected range for heterotrophic bacterial reactions. For G_P = 0.05 to 0.2 day^{-1} which is characteristic of the summer average epilimnion values and $\rho = 0.5$ as an estimate of the respired and excreted fraction that is unavailable, the range of δ is 0.1 - 2.5 corresponding to a range in p_u/p_T of 30% to 90%. The large unavailable fraction corresponds to a low recycle rate and a high algal growth rate and therefore, at steady state, a high respiration plus grazing rate, whereas fast recycle and slow growth result in the low fraction unavailable. It is probable that under this condition the available and zooplankton fractions become significant, the approximations $p_i/p_T << 1$ and $Z'/p_T << 1$ are no longer reasonable, and eq. (3) is not applicable. This suggests that p_u/p_T may not decrease as low as 30%.

For these kinetic equations and assumptions it is also possible to calculate the algal phosphorus fraction and the chlorophyll a/total phosphorus ratio, P/p_T. The latter follows from the approximation: $a_{pP}P + p_u \simeq p_T$ and eq. (54):

$$\frac{P}{p_T} \simeq \frac{1}{a_{pP}} \frac{\delta}{1 + \delta} \tag{56}$$

The importance of the stoichiometric coefficient a_{pP} is clearly evident in this equation as is the effect of δ.

RECYCLE RATE AND CHLOROPHYLL CONCENTRATION

The relationship, eqs. (54) and (55), between recycle rate, K, the fraction of respired and excreted phosphorus that is unavailable, ρ, and the ratio of unavailable to total phosphorus suggests that the observed variations in the latter be used to investigate variations in the former. As mentioned previously no direct measurement of unavailable phosphorus is available since the detrital and algal particulate phosphorus are not separable. However if only soluble phosphorus is considered then unavailable phosphorus is equivalent to dissolved organic phosphorus which can be estimated as total dissolved minus soluble reactive phosphorus, and the ratio p_u/p_T for soluble phosphorus can be calculated. Alternately if a phosphorus to chlorophyll ratio is assumed then the algal bound phosphorus can be estimated and a direct calculation of $p_u p_T$ is possible with the additional assumption that Z' is negligible.

TABLE 5. EXPERIMENTALLY DETERMINED NUTRIENT RECYCLE RATES

Organism	Variable	Rate (day^{-1})	θ	Reference
Puget Sound Net plankton	PO_4-P	0.016	-	Grill & Richards
	NH_3-N	0.019	-	"
	S . Si	0.017	-	"
Variable	Non-refractory COD	0.04 ± 0.034	-	Jewell & McCarty
Axenic culture with bacterial seed	Non-refractory COD	0.015 - 0.07	1.04 - 1.09#	"
Variable (anaerobic decomposition)	Non-refractory COD	0.022 ± 0.007	1.057#	Foree & McCarty
Chlorella vulgaris	Particulate COD	0.013 - 0.078	-	DePinto & Verhoff
P-starved	PO_4-P	0.03 - 0.04*	-	"

* calculated using PO_4-P/Chl_a = 0.5, C/Chl_a = 100, C/dry wt. = 0.40

# temperature dependence of the form θ^{T-20} for T in °C

Both of these methods can be used to estimate p_u/p_T. This has been done for the various data sets for which the appropriate measurements are available. The procedure is to average the epilimnion observations during the period of stratification for the years indicated. The well mixed basins, Western Lake Erie and Saginaw Bay, are analyzed for the periods employed for the rest of that lake. The idea is to conform to the assumptions of the simple analysis of the previous section, namely steady state and constant parameters, by using long time averages. Admittedly, this is rather crude but the results are quite interesting.

The data used for the calculations are given in Table 6. Plots of the ratio of soluble unavailable to total soluble phosphorus and the ratio of estimated total unavailable to total phosphorus versus chlorophyll a are shown in fig. 19. The results suggest an inverse relationship between the unavailable fraction of both the soluble and total phosphorus and chlorophyll. The exceptionally large Saginaw Bay value for the soluble fraction is probably the result of the influence of inputs which have been neglected in the simple analysis of the previous section.

For the computations that follow the relevant plot is that relating total unavailable phosphorus to total phosphorus, consistent with the phosphorus species considered in the theoretical analysis. The decrease in the fraction unavailable: from $p_u/p_T = 0.8$ for the low chlorophyll basins, to $p_u/p_T = 0.7$ for the intermediate basins (~ 5 μg Chℓ-aℓ) to $p_u/p_T = 0.65$ for the basins with higher chlorophyll concentrations, suggest that the recycle rate is influenced by the chlorophyll a concentration.

This 20 percent change in the ratio of p_u/p_T over an order of magnitude increase in chlorophyll a takes on added significance when one considers that there is only minor variability in the data given in Table 6. For Lake Ontario, for instance, the standard error is within 1.0 - 8.5% of the mean values listed for the component variables of the calculation, total, dissolved, and available phosphorus and chlorophyll a, with an average of some 1,000 data points from four lakewide cruises used as part of the computation.

That such a relationship should exist can be seen from the following reasoning: If the agents of the recycle reaction are heterotrophic bacteria which convert unavailable phosphorus to available phosphorus as a byproduct of their metabolic activity, and if the major source of carbon for the energy and synthesis reactions of the bacteria is the detrital carbon produced by the algal respiratory and excretion reactions, it is reasonable to expect that the bacterial biomass increases as the source of this detrital carbon, namely the standing stock of algae, increases. Evidence that bacterial biomass increases as chlorophyll a increases has been reported for a series of Canadian Lakes [58] and for Lake Huron [59]. Although the relationships are different for the different sets of data, the trend is clear in both cases. Evidence from other studies [60,61,62] indicates that the seasonal trends of chlorophyll and bacteria, although not in perfect phase, tend to follow the same pattern.

TABLE 6. DATA USED FOR RECYCLE RATE ANALYSES

LOCATION*	Total]1] PO_4-P (μg/ℓ)	Total[2] Diss. PO_4-P (μg/ℓ)	Soluble[3] Reactive PO_4-P (μg/ℓ)	Chℓ-a[4] (μg/ℓ)	Soluble(1) p_u/p_T	Estimated(2) p_u/p_T	G_P (day^{-1})	Y (°C)
W. Lake Erie(WB) 1971, 1975 Day 180-240	44.5	14.5	7.0	15.8	0.517	0.664	0.138	22.4
C. Lake Erie(CB) 1971, 1975 Day 180-240	21.3	7.5	3.25	5.5	0.573	0.718	0.136	20.9
E. Lake Erie(EB) 1971, 1975 Day 180-240	18.8	7.5	2.3	3.0	0.693	0.80	0.128	20.5
S. Lake Huron(SH) 1971, 1974 Day 210-270	5.53	2.54	0.62	1.24	0.756	0.775	0.0597	17.9
Saginaw Bay(SB) 1971, 1974 Day 210-270	34.2	6.92	2.21	20.1	0.682	0.630	0.135	19.1
Lake Ontario(ON) 1972 Day 140-262	18.4	9.88	3.63	4.48	0.660	0.696	0.125	12.9

(1) Soluble p_u/p_T = ([2]-[3])/[2]

(2) Estimated p_u/p_T = ([1]-[3]-a_{pP}[4])/[1] with a_{pP} = 0.5 μg PO_4-P/μg Chℓ-a

* Epilimnion waters

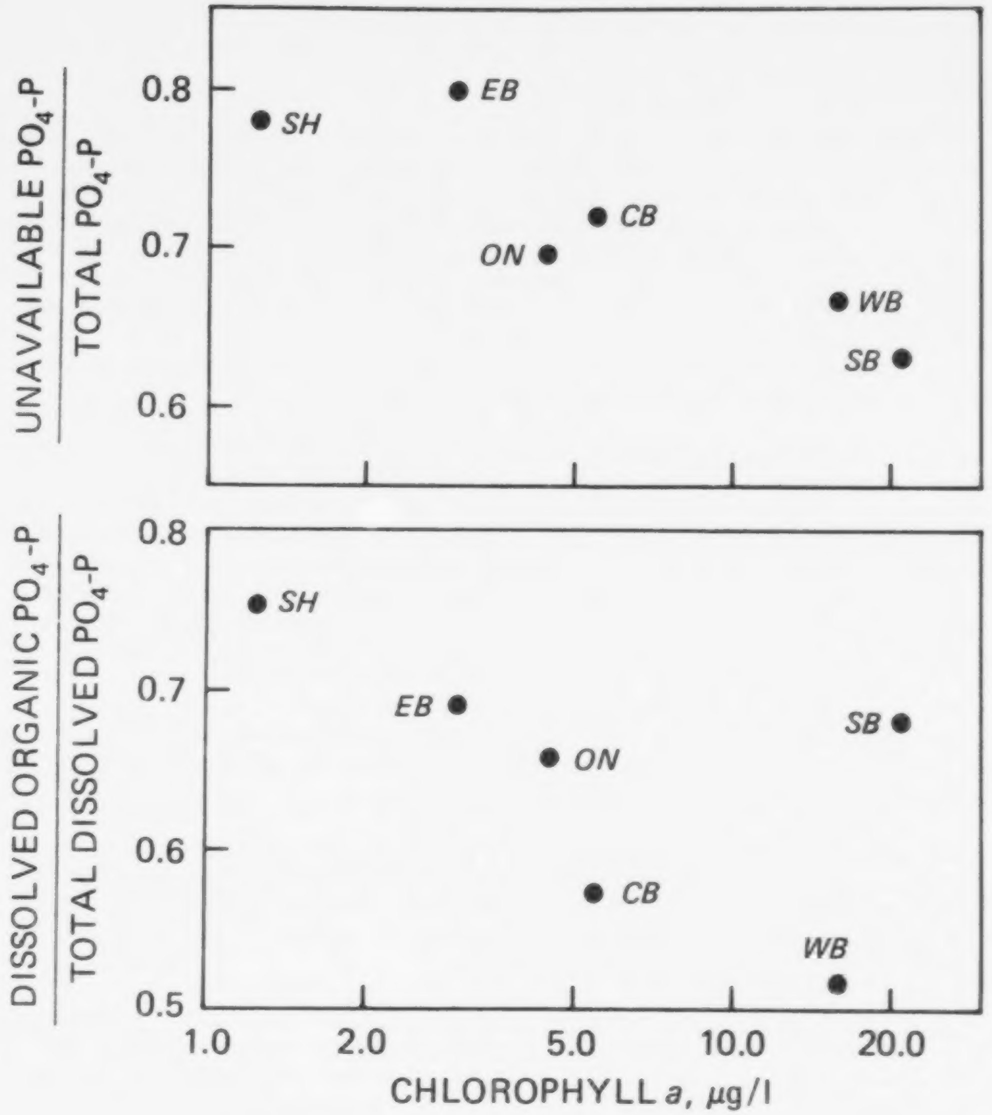


Figure 19. Variation of the ratio of estimated unavailable to total phosphorus and of dissolved organic to total dissolved phosphorus ratio with chlorophyll. See Table 6 for legend.

On the other hand, it is also known that certain species of algae can metabolize dissolved organic phosphorus directly [50] in which case the quantity of unavailable phosphorus would tend to decrease as chlorophyll increases. Hence if either or both these mechanisms are active the result is an increased recycle rate as chlorophyll increases.

Alternately, the decrease in the ratio of unavailable to total phosphorus as chlorophyll increases could be related to a decrease in, ρ, the unavailable fractions respired and excreted. The mechanism is related to the fraction of algal phosphorus that is labile and quickly available $(1-\rho)$ and that which is structurally bound and unavailable, ρ. In oligotrophic situations it is probable that a smaller fraction is labile and ρ is larger than in eutrophic settings where ρ is smaller. This suggests that ρ would decrease as chlorophyll increases. Based on eqs. (54) and (55), it is not possible to distinguish between K increasing and/or ρ decreasing as chlorophyll increases since they occur as a ratio (eq. 55).

All these mechanisms are known to occur and influence the relationship between unavailable to total phosphorus and chlorophyll. The question is: how to modify the equation structure to account for the observations. A number of approaches are possible. Bacterial biomass can be included directly as a state variable with a governing differential equation [103]. The problem is that in most cases observations of bacterial biomass are not available and the kinetic constants obtained from a calibration with unobserved state variables are likely to be quite tentative and uncertain.

The inclusion of state variables which partition the internal algal pools of phosphorus is also possible [99] but again these cellular concentrations are unobservable and add to the uncertainty of the calibration, while also increasing the realism of the formulation.

An alternate approach, which has the attraction of simplicity, is to establish an empirical relationship between recycle rate and chlorophyll. As shown subsequently this adds only one more unknown kinetic coefficient to the formulation and no unobservable state variables. For this reason this latter approach seems appropriate.

With the data in fig. 19 interpreted as suggesting that the recycle rate is chlorophyll dependent with ρ constant it is necessary that the functional form of the dependence be established. The relationships which span the expected dependency for the recycle rate coefficient are:

First order recycle: $$K = K'(T) \tag{57a}$$

Second order recycle: $$K = K''(T)P \tag{57b}$$

Saturating recycle: $$K = K'(T)\frac{P}{K_{mr} + P} \tag{57c}$$

with conventional θ temperature dependence for the rate constants $K'(T)$ and $K''(T)$. First order kinetics, which are the conventional formulations for the transformation of organic to inorganic nutrient forms in estuaries [63] and previous lake models [48] assume a recycle rate constant that varies with temperature only. Second order recycle assumes that the rate of recycle is proportional to the phytoplankton biomass present as well as the amount of unavailable nutrient. In laboratory experiments, pure cultures with bacterial seeding appeared to follow a second order dependency [56]. Saturating recycle is a compromise between these two mechanisms: a second order dependency at low chlorophyll concentrations when $P << K_{mr}$, where K_{mr} is the half saturation constant for recycle, and first order recycle when the chlorophyll greatly exceeds the half saturation constant. Basically this parameterization slows the recycle rate if the algal population is small but does not allow the rate to increase continually as chlorophyll increases. The assumption is that at higher phytoplankton chlorophyll concentrations other factors are rate limiting the recycle kinetics so that it proceeds at its maximum first order rate.

Two tests of these forms for the recycle kinetics have been made. The first utilizes the expected relationship between p_u/p_T and $\delta = K/\rho G_p$ given by eq. (54). The growth rate G_p is calculated using the conventional expressions and the results of seasonal calculations, [37,48] and $\rho = 0.5$ is used for all basins. In addition it is assumed that $\theta = 1.08$ for this reaction. Using the information in table 6, it is possible to calculate δ for each hypothesized recycle mechanism:

$$\text{First Order:} \qquad \delta = \frac{K'\theta^{T-20}}{\rho G_P} \tag{58a}$$

$$\text{Saturating:} \qquad \delta = \frac{K'\theta^{T-20}}{\rho G_P} \, \frac{P}{K_{mr} + P} \tag{58b}$$

$$\text{Second Order:} \qquad \delta = \frac{K''\theta^{T-20}}{\rho G_P} P \tag{58c}$$

and to compare the observed ratio, p_u/p_T, for this basin with the expected ratio: $1/(1+\delta)$. The results are shown in fig. 20 for $K' = 0.04$ day^{-1}, $K_{mr} = 5$ μg Chℓ-a/ℓ, and $K'' = 0.00843$ day^{-1}/μg Chℓ-a/ℓ which appears reasonable from the calculations to be discussed subsequently. Consistent results are obtained only if the saturating recycle formulation is used to calculate δ. Neither first nor second order kinetics are appropriate since the observations are not consistent with the expected theoretical result, namely that $p_u/p_T = 1/1+\delta$. Thus in order to be consistent with observations in the various basins it is necessary to adopt a saturating recycle rate as the functional dependency on chlorophyll.

The second test of this formulation is a comparison of seasonal calculations and observations in the various basins which is discussed below.

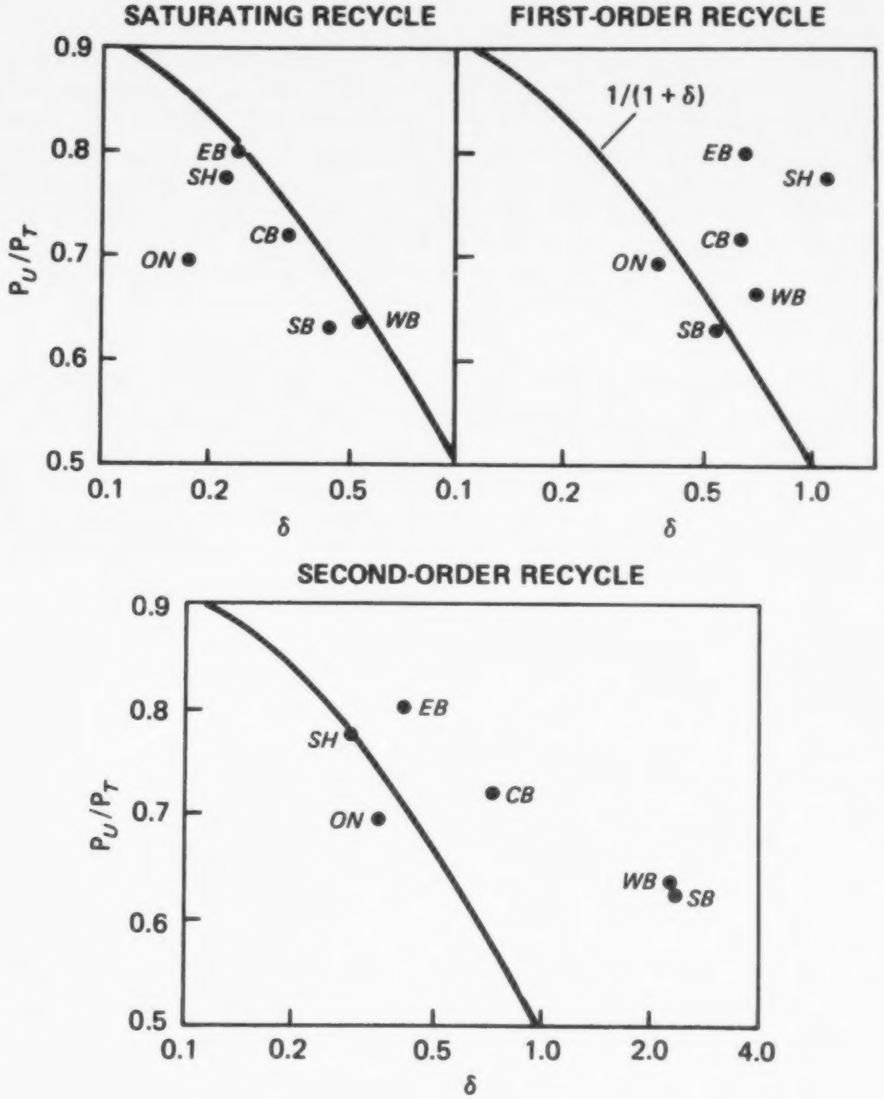


Figure 20. Comparison of observed and calculated ratio of unavailable to total phosphorus for saturating (eq. 58b), first order (eq. 58a), and second order (eq. 58c) nutrient recycle kinetics.

SECTION 7

DATA

The credibility of model calculations is determined, in large measure, by their agreement with observations. Besides the obvious constraints that the model should behave reasonably well and predict general patterns such as spring phytoplankton growth, this is perhaps the only external criteria which is available to determine the validity and hence the utility of a complex eutrophication model. A comparison to actual data indicate if the approximations used in the model adequately represent the real situation. With this in mind, a detailed review of available data for Lake Huron and Saginaw Bay is presented and from these data a set of aggregated data were generated for use in calibration.

HISTORICAL DATA

Prior to 1971, not much comprehensive limnological data had been gathered for Lake Huron, and those data which were available fell short of providing the substantial data base necessary for water quality modeling efforts. Data for Saginaw Bay were even more scarce. One observer, reviewing historical data for the bay, noted that "presently, the necessary data for verification (of water quality models) does not exist."[3]

The data summary presented in Table 7 encompasses all of the major Lake Huron surveys which were available for review. One of the earliest surveys of Lake Huron was that undertaken by Ayers, et al. [16] in the summer of 1954. This survey consisting of three cruises during which a few chemical parameters were measured (Ca, Mg, SiO_2), but of prime interest are the measurements of current magnitudes and directions made using drift bottles. To date, this is still one of the best sources of flow patterns for Lake Huron and its applicability to this modeling effort has been discussed in relation to transport regime estimation (section 5). Drift bottle current measurements were also made by the U.S. Fish and Wildlife Service in 1956 [64]. Other analyses of Lake Huron circulation are also available [65,66,67].

Commencing in 1960 and continuing through 1970, the Great Lakes Institute (GLI) of the University of Toronto conducted several surveys of Lake Huron [68]. These consisted of temperature, geophysical, meteorological, internal wave and synoptic surveys. GLI data reports [69-73] include comprehensive weather information and lakewide temperature data.

In 1965, the FWPCA sampled Saginaw Bay and the Southern Lake Huron tributary area [74]. The stations in the bay were sampled twice a month during the summer and fall of 1965. These data are available through STORET. Data from similar surveys made by the FWPCA during the period 1967-1970 [75,76,77, 78] were also reviewed through STORET. In addition, tributary measurements,

TABLE 7. HISTORICAL DATA FOR LAKE HURON

Time Period	Coverage	Agency	No. of Stations	Parameters Measured
1954 (6/28, 7/27.) (8/25)	main lake	GLRD	80-94	Transparency, Mg, SiO_2 temperature, Ca, conductivity, currents
1956 (6/5 - 11/14)	mainly Saginaw Bay	USFWS		Drift bottle current measurements
1960 (6/26, 10/2) (11/22, 12/10)	main lake	GLI	15-83	Weather, transparency, color, DO, pH, temperature, conductivity, alkalinity, phenois, coliforms
1960 (10/7, 11/22) (11/25)	Georgian Bay	GLI	6-56	"
1961 (6/25, 9/5) (10.10, 12/15)	main lake	GLI	58	"
1961 (7/4,7/8,87) (9/9,10/15) (12/73)	Georgian Bay	GLI	45	"
1962 (4/10,5/22,7/23) (8/25,9/25,10/2)	main lake	GLI	45	"
1962 (4/19,5/26/8/21) (9/18,12/6)	Georgian Bay and North Channel	GLI	15-45 6	"

TABLE 7 (Cont'd)

Time Period	Coverage	Agency	No. of Stations	Parameters Measured
1963 (5/4,6/17,7/15) (8/13,9/16,10/29)	main lake	GLI	59	"
1963 (5/1,9/10)	Georgian Bay	GLI	43-48	"
1964 (4/29,6/8,7/6) (8/17,11/16)	main lake	GLI	61	"
1964 (6/24,7/25,8/20) (9/20)	Georgian Bay	GLI		"
1965	Entire lake	FWPCA	120	PO_4, Cl, NH_3, NO_3, DO transparency, phytoplankton populations
1965 (6/00,12/00)	Saginaw Bay	FWPCA	24	DO, BOD, NH_3-N, Org N, NO_3-N, NO_2-N, PO_4,solids Cl, pH, phenols, COD
1966 (6/00,8/00)	Saginaw Bay	FWPCA	47	DO, temperatures, secchi.
1967 (7/26,8/1)	Entire lake	FWPCA	55	DO, NH_3-N, Org N, NO_3-N NO_2-N, PO_4, Cl, pH, COD, temp, conductivity, alkalinity
1968 (9/6,9/11)	main lake	FWPCA	45	Temperature, Secchi, cloud cover, euphotic zone, phytoplankton biomass

TABLE 7 (Cont'd)

Time Period	Coverage	Agency	No. of Stations	Parameters Measured
1968 (8/5-8/13)	Entire lake	CCIW	100	Secchi, temp., turbidity, pH, alkalinity, DO, PO_4, NO_3, SO_4, F, CL, SiO_2, hardness, Ca, Mg, K, Na, coliforms, chlorophyll
1969 (7/1-7/30) (8/13)	lower Saginaw Bay	FWPCA	13	temp., pH, DO, conductivity, phenols, Cl, SO_4, alkalinity, NO_3, NH_3-N, Org-N, PO_4, turbidity, Fe, solids, coliforms
1969 (9/22-9/29)	Entire lake	CCIW	100	Secchi, color, temp. turbidity, sp-conductance, DO, total phosphate, NH_3-N, NO_3-N, SiO_2, coliforms
1969 (11/8-12/06)	Entire lake	CCIW	97	Secchi, color, temp. turbidity, conductivity, DO, alkalinity, SO_4, Cl, hardness, Ca, Mg, K, Na, HCO_3, chlorophyll a
1970 (7/27-7/29)	Entire lake	EPA	42	Temp., pH, alkalinity, conductivity, turbidity, SO_4, Cl, Org N, NH_3-N, NO_2-N, PO_4.

TABLE 7 (Cont'd)

Time Period	Coverage	Agency	No. of Stations	Parameters Measured
1970 (5/11-5/18)	Entire lake	CCIW	100	Secchi, color, temp., turbidity, conductivity, alkalinity, DO, chlorophyll, Org C, HCO_3, PO_4, NH_3-N, NO_3-N SO_4, Cl, SiO_2, metal ions, coliforms
1970 (9/29-10/7)	Entire lake	CCIW	101	Secchi, color, temp. turbidity, conductivity, pH, alkalinity, DO, PO_4, NH_3-N, NO_3-N, SO_4, Cl, SiO_2, metal ions, coliforms
1970	Saginaw Bay and Western Lake Coast	GLRD	26	DO, SiO_2, NO_3-N, NH_3-N, PO_4, conductivity, pH, transparency, alkalinity, Ca, Cl, SO_4, chlorophyll, carbon fixation and assimilation
1971 (4/19-12/06)	Entire lake	CCIW	46	chlorophyll a, primary prouctivity, assimilation ratios
1971 (4/19-12/06)	Entire lake	CCIW		Secchi, color, temperature, turbidity, conductivity, DO, alkalinity, Total Phosphorus, NH_3, NO_2, NO_3, SiO_2

coupled with the lake surveys [79-85] and combined with USGS flow data, can provide mass loading information.

In 1968, the Canada Centre for Inland Waters (CCIW) commenced synoptic surveys of Lake Huron. Their Limnological Data Reports [86,87] provide data from cruises in August of 1968 and September and November of 1969. Two cruises in 1970 were made during May and October. These surveys included data for several parameters and the spatial and depth coverage of the lake is extensive. Another 1970 cruise was conducted by the Great Lakes Research Division of the University of Michigan [2] concentrating mainly in Saginaw Bay and the Michigan shoreline region.

In order to properly calibrate a eutrophication model, data sets which include phytoplankton chlorophyll and nutrient data measured over the entire lake, in depth, and with adequate temporal coverage are needed. The historical surveys discussed above are not adequate for this purpose because they failed to meet one or several of these criteria.

Calibration Data

The data base used for calibration of the model is derived mainly from three sources:

(1) Canada Centre for Inland Waters (CCIW)
(2) Great Lake Research Division (GLRD), University of Michigan
(3) Cranbrook Institute of Science (CIS)

These sampling surveys together with a compilation of background material and an evaluation of sources and characteristics of material inputs form an integral part of the IJC Upper Lakes Reference Study [10], which should be consulted for a more detailed review of procedures and results.

Data from the CCIW cruises are available for two survey years, 1971 and 1974. Table 8 lists the sampling dates and parameters measured on these cruises. The 1971 surveys [88] sampled at least 78 stations per cruise and the 1974 surveys [89] sampled 45 stations, excluding the North Channel. Both surveys have only one sampling station in inner Saginaw Bay. Chlorophyll-a, primary production, and phytoplankton composition for the 1971 cruises have been analyzed [90,91,92] and zooplankton distribution for these same cruises have also been studied [93].

The 1974 GLRD Lake Huron surveys [94] sampled a range of 36-44 stations for eight cruises. These stations are concentrated in southern Lake Huron and the outer reaches of Saginaw Bay. Sampling dates and parameters measured on these cruises are listed in Table 9.

Table 10 lists the cruise dates and measured parameters for the 1974 CIS surveys of Saginaw Bay [95]. These surveys form the most comprehensive study which has been undertaken for Saginaw Bay and fills many voids in the historical data base for the bay. A total of 59 bay stations were sampled, some of which are at the mouth of the Saginaw River, including 4 water intake stations.

TABLE 8. CCIW LAKE HURON SURVEYS

YEAR	CRUISE	DATE	PARAMETERS MEASURED ON ALL CRUISES
1971	1	4/19-4/28	Secchi, Temperature, Turbidity, pH,
1971	2	5/17-5/25	Specific Conductance, Chlorides,
1971	3	6/15-6/28	D.O., Silica
1971	4	7/19-7/27	NH_3-N, NO_2+NO_3-N, NO_2-N,
1971	5	8/23-8/30	Inorganic Carbon[*] Total Carbon[*],
1971	6	9/27-10/4	Organic Carbon[*], Chlorophyll,
1971	7	10/27-11/3	Total P, Dissolved P,
1971	8	11/29-12/6	Reactive P.
1974	1	4/23-4/28	Secchi, Temperature,
1974	2	5/14-5/18	Specific Conductance, pH,
1974	3	6/22-6/28	Alkalinity, Particulate
1974	4	7/22-7/28	Organic Carbon[*], D.O.,
1974	5	8/26-9/2	Total P, Soluble P, Reactive
1974	6	9/30-10/6	P, total particulate
1974	7	12/4-12/10	Nitrogen[*], NO_3+NO_2-N, total N[*], SO_4, Chlorides, Silica, Chlorophyll

[*] Not measured on all cruises.

TABLE 9. 1974 GLRD LAKE HURON SURVEYS

CRUISE	DATE	PARAMETERS MEASURED ON ALL CRUISES
1	4/28-5/3	Secchi, Temperature, pH, Conductivity, SiO_2, NO_3-N, NH_3-N, Total P, Soluble P, SO_4, Chlorides, Chlorophyll Phaeophytin fraction, Alkalinity, carbon^{14} uptake, particle counts
2	5/14-5/17	
3	6/04-6/08	
4	6/17-6/25	
5	7/17-7/22	
6	8/26-8/31	
7	10/08-10/12	
8	11/10-11/14	

TABLE 10. 1974 CIS SAGINAW BAY SURVEYS

CRUISE	DATE	PARAMETERS MEASURED ON ALL CRUISES
3	2/18-2/21	Temperature, Secchi,
4	3/25	Conductivity, DO, pH,
5	4/17-4/20	Alkalinity, NH_3-N,
6	4/28-4/30	Kjeldahl-N, NO_2+NO_3-N,
7	5/13-5/17	Total P, Dissolved P_2
8	6/02-6/05	Dissolved Ortho-P, Ca,
9	6/18-6/22	Mg, Na, K, Chlorides,
10	7/08-7/10	SO_4, Silics, Chlorophyll,
11	7/25-7/27	Phaeophytin
12	8/25-8/27	
13	9/18-9/20	
14	10/06-10/08	
15	11/11-11/14	
16	12/16-12/18	

TABLE 11. SURVEY STATIONS AND MODEL SEGMENTS

Model Segment No.	Depth Range (Meters)	1971 CCIW*	1974 CCIW**	1974 GLRD	1974 CIS
1	0-15	37-48 50-100	108-134 157-167	ND	ND
2	0-15	1-5, 7-30, 33-36, 49	101-105 107 166	1-7, 9-11, 13-15, 20-26, 36-58, 60, 63-65,	42-53 57,58
3	0-6 (all depths measured used for bay stations)	31,32	106	ND	2-40, 56 59
4	15-bottom (only values @ > 15 meter depth used)	Same as Seg. 1	Same as Seg. 1	ND	ND
5	15-bottom (only values @ > 15 meter depth used)	Same as Seg. 2	Same as Seg. 2	Same as Seg. 2	Same as Seg. 2

* CCIW Permanent Station Numbers

** Chlorophyll Values for 1974 are integrated samples (usually to 20m) these values are used for the top layer (0-15m) segments only

ND No Data

Figure 21 shows the lake coverage provided by the surveys cited. Saginaw Bay, northern, and southern Lake Huron are adequately covered by the sampling stations as a group. They are used collectively since the CCIW data gives adequate coverage of the northern and southern lake but not of Saginaw Bay, CIS surveyed only in the bay, and GLRD concentrated the southern lake and outer bay. Taken together, the 1974 surveys provide the most comprehensive Lake Huron water quality to date and their utility for the calculations to be presented below cannot be overemphasized. Without such comprehensive data, calculations of this complexity could not be adequately calibrated.

Data Reduction

The data base resulting from an aggregation of the surveys is quite large. Altogether there are a total of 35 cruises and approximately 225 individual sampling stations measured over a range of depths. The first step in processing these data is to match the sampling stations to the model segmentation. Using cruise maps from each of the four surveys, the individual stations are assigned to the appropriate model segment as shown in Table 11. The cruise mean and standard deviation for each variable utilizing all stations within a segment are computed. These values for each survey are then overplotted and the result is a set of calibration data for each model segment for all parameters being considered.

Aggregation and statistical reduction of data described above has been found to be appropriate and, in fact, quite necessary. As an illustration of the variation which may be encountered when dealing with data not only from different locations but different agencies as well, plots were made of surface values for several parameters measured by different groups at essentially the same location in the lake. Three separate comparisons are presented. Table 12 lists the overlapping stations and figs. 22-24 show the results. Parameters near the limit of sensitivity of the test employed: reactive and total dissolved phosphorus, ammonia, and to a certain extent, chlorophyll show large variations whereas the nitrate measurements are in virtual agreement. Total phosphorus and reactive silica are in agreement for certain stations but not at others. The possible causes of these variations are differences in sampling methods if a consistent difference is obtained; for example, soluble reactive phosphorus at the northern and southern Saginaw Bay comparison stations; and changes in actual concentrations over short time scales due to the transient nature of the circulation and mass loading for the locations chosen.

The latter effect must be smoothed out of the data since the calculations are not designed to reproduce short time scales but rather the longer monthly and seasonal changes. Thus aggregation of stations, comparison to several sources where they exist, and statistical reduction to means and standard deviations are necessary in order to smooth the variations encountered.

The results of the aggregation and statistical reduction of the 1971 and 1974 data sets are shown in figs. 25-35 for all the segments considered. The comparison is made between the two years and between the different

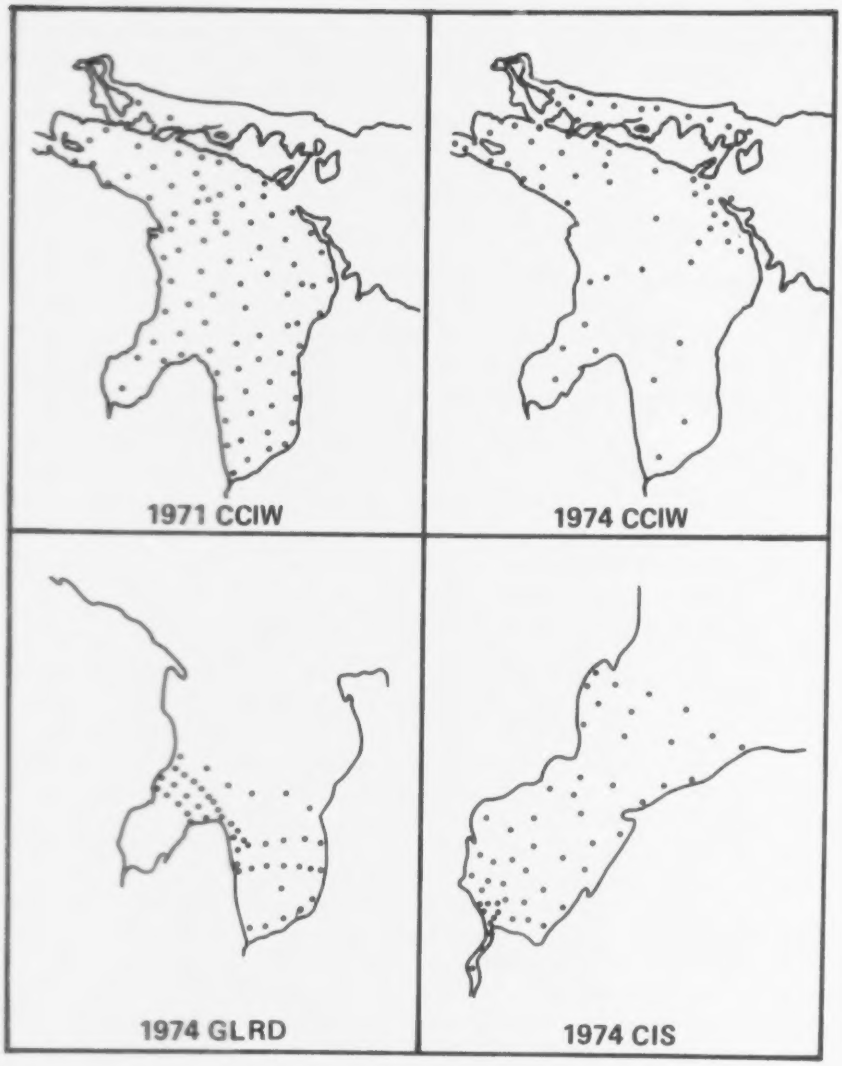

1971 CCIW
1974 CCIW
1974 GLRD
1974 CIS

Figure 21. Sampling station locations for the major data sets used in this report. These correspond to the tabulations in Tables 8 - 10.

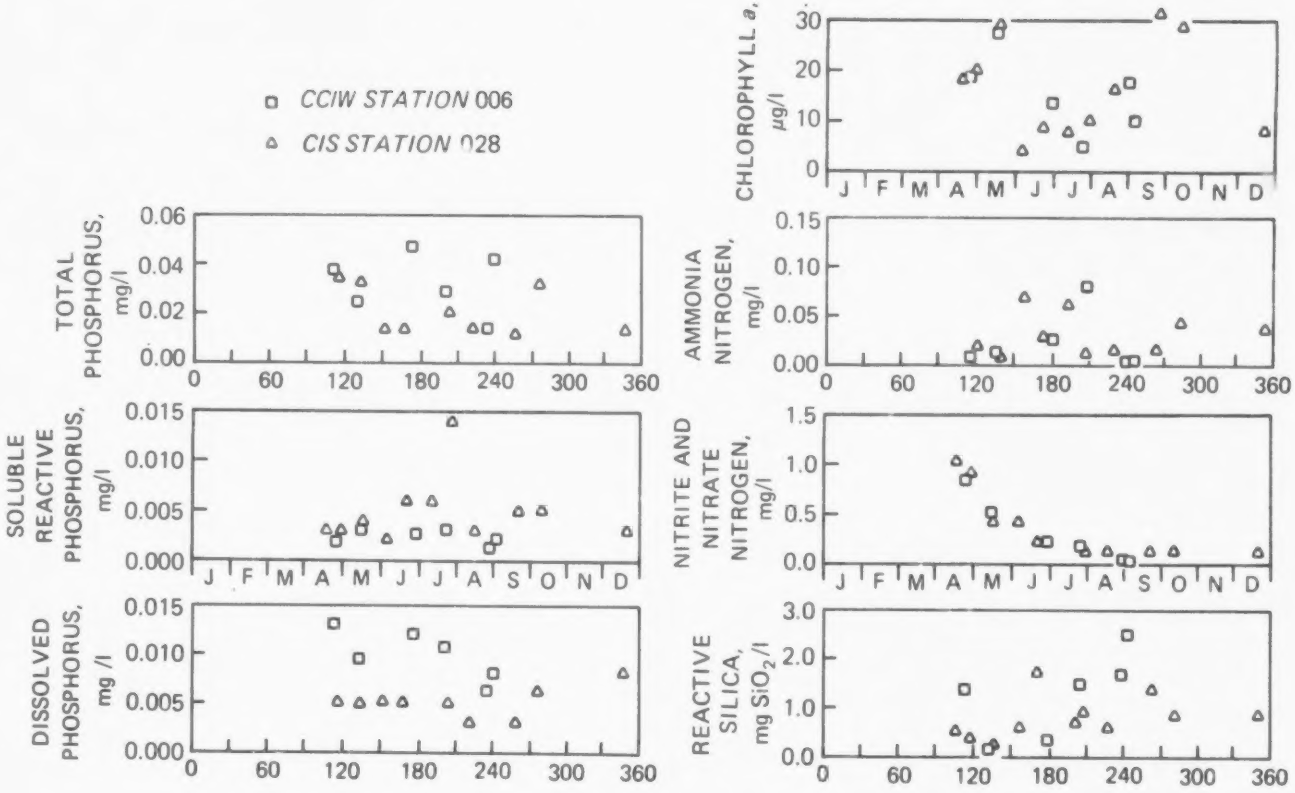


Figure 22. Comparison of data taken by CCIW, CIS, and GLRD at approximately the same location in Inner Saginaw Bay

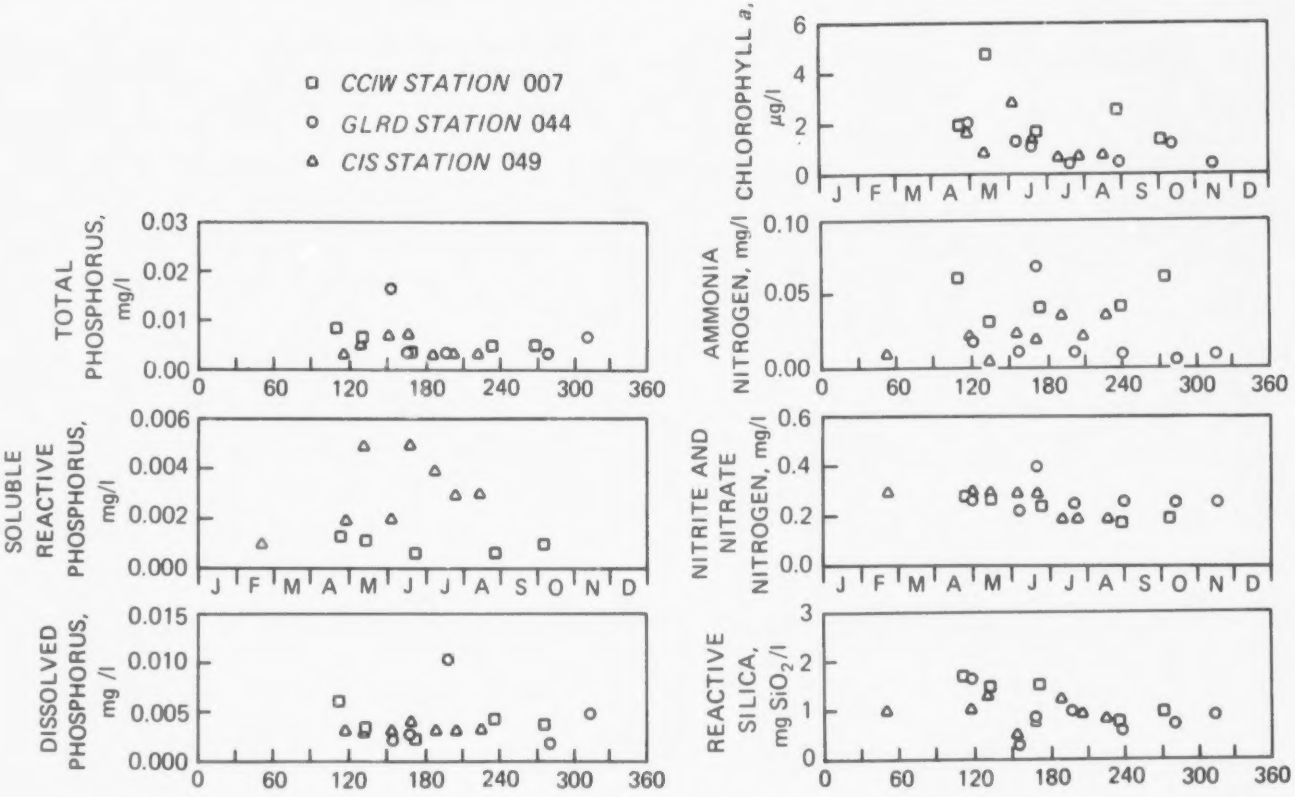


Figure 23. Comparison of data taken by CCIW, CIS, and GLRD at approximately the same location in Northern Saginaw Bay

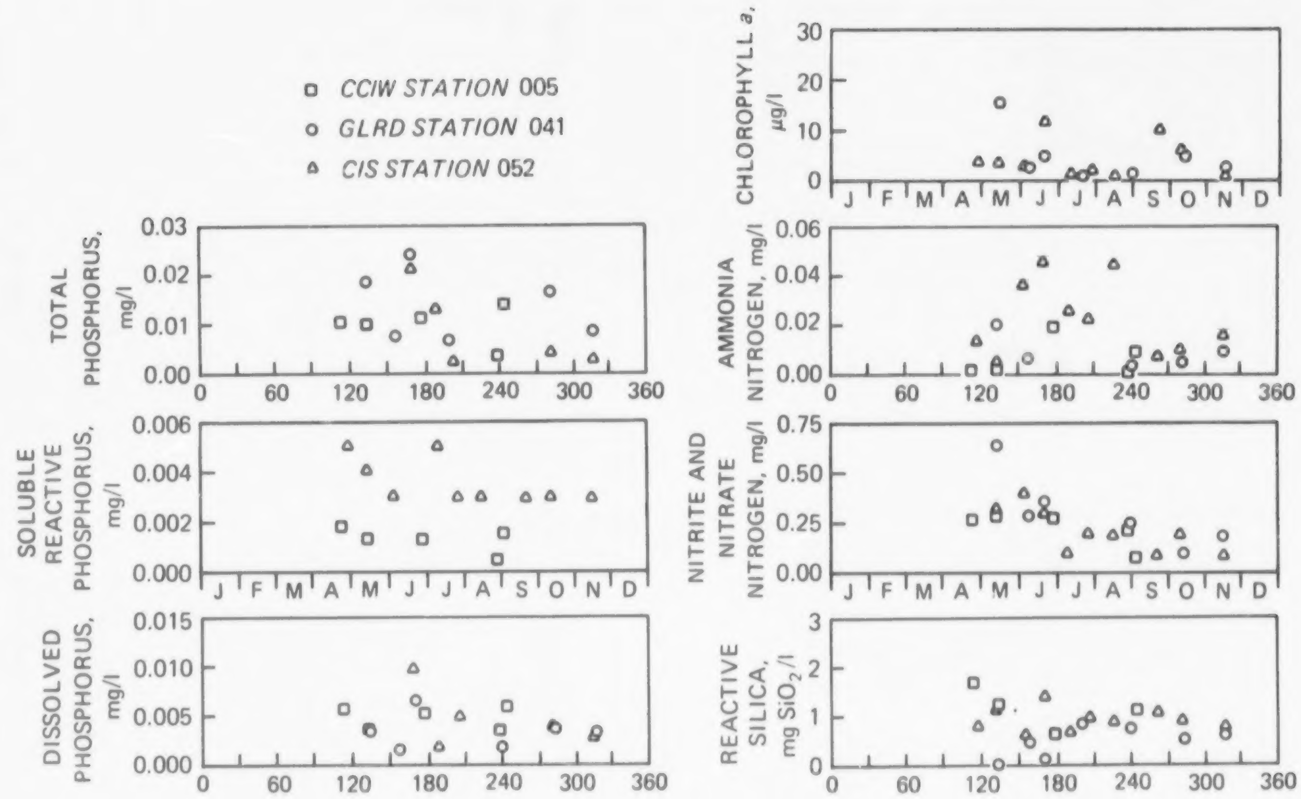


Figure 24. Comparison of data taken by CCIW, CIS, and GLRD at approximately the same location in Southern Saginaw Bay

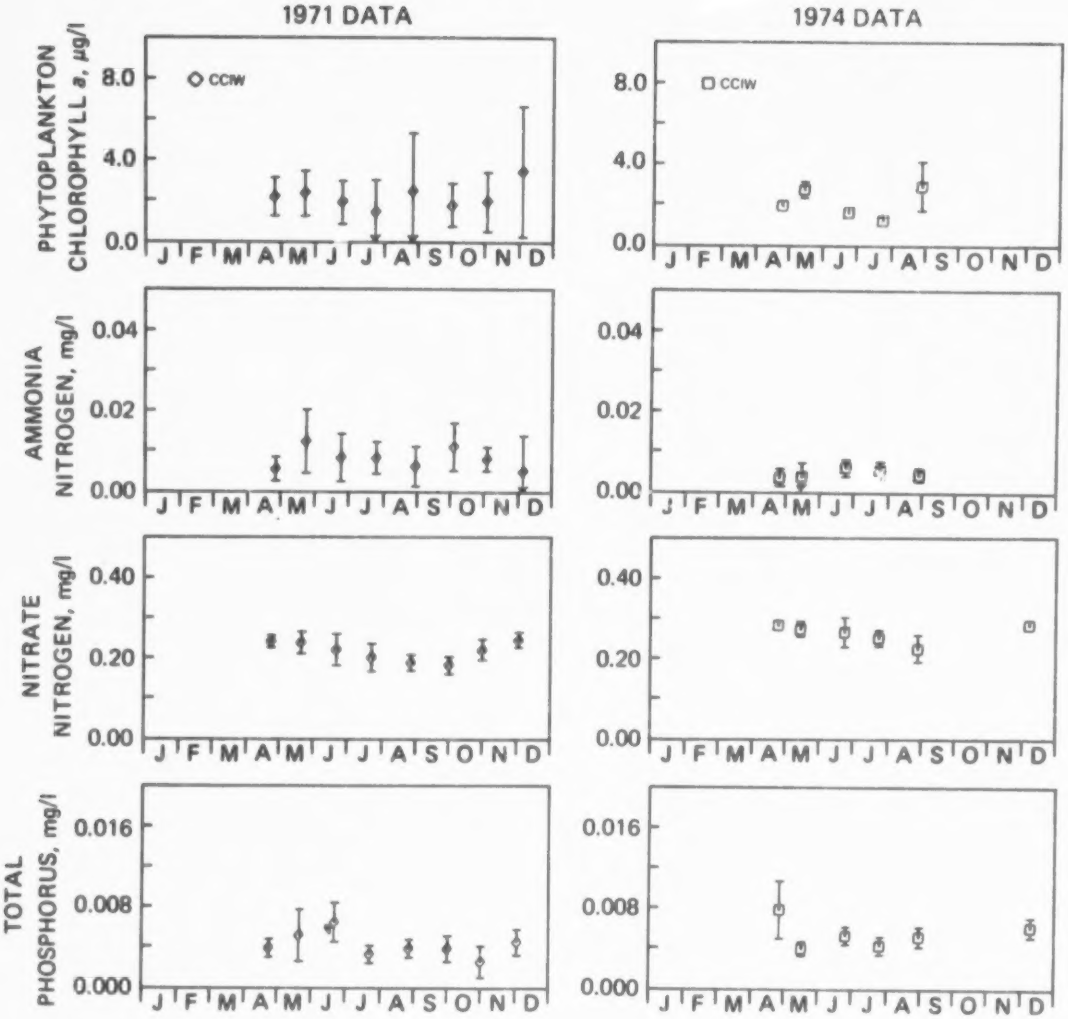


Figure 25. Model Calibration Data (Segment 1)

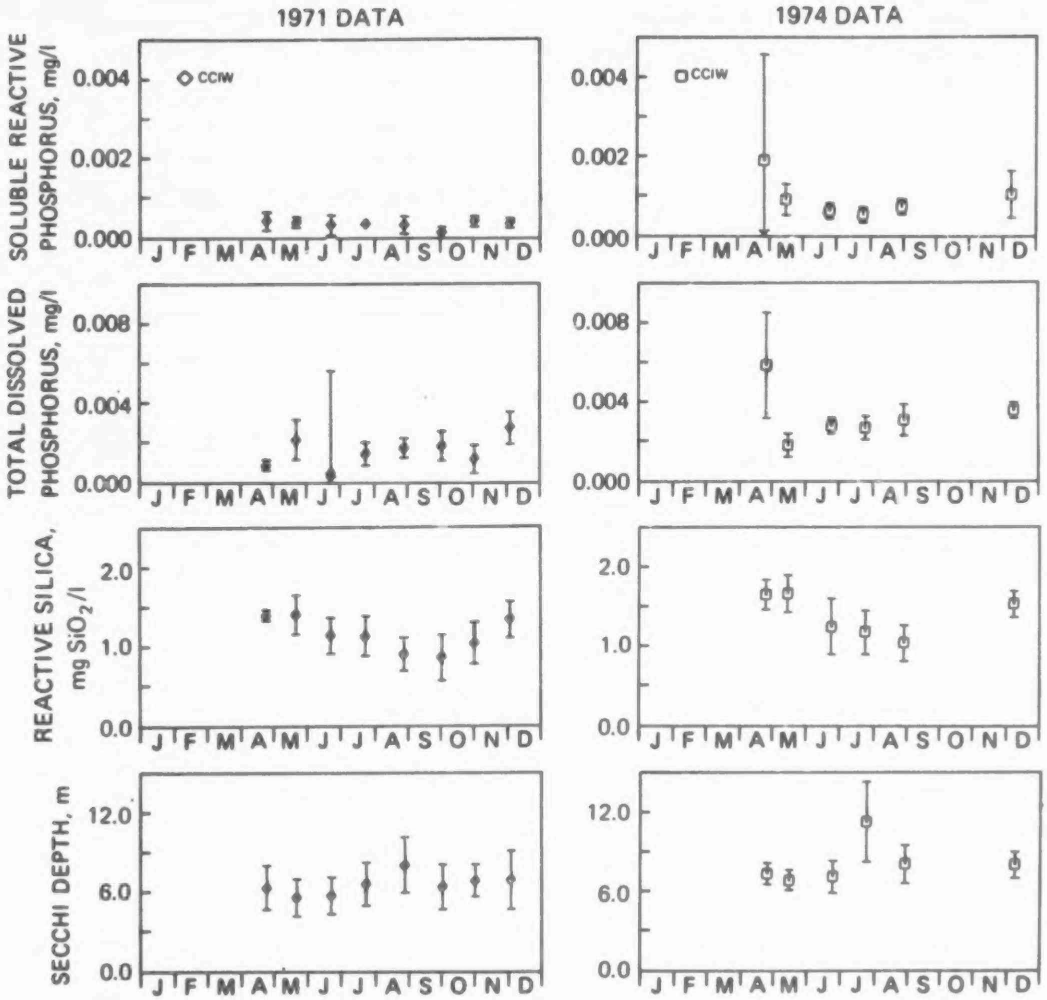


Figure 26. Model Calibration Data (Segment 1)

TABLE 12. INTER-SURVEY STATION COMPARISONS

AGENCY	STATION NO.	LATITUDE	LONGITUDE	LOCATION
'74 CCIW	006	43°51'30"	83°40'12"	Inner Saginaw Bay
CIS	028	43°51'35"	83°40'25"	
'74 CCIW	007	44°12'24"	83°23'00"	Northern Saginaw Bay
CIS	049	44°12'40"	83°22'40"	
GLRD	44	44°11'42"	83°20'36"	
'74 CCIW	005	44°04'16"	83°05'08"	Southern Saginaw Bay
CIS	052	44°04'10"	83°04'50"	
GLRD	41	44°03'18"	83°02'54"	

agency sources if they overlap. The primary purpose of this comparison is to investigate the differences in the two years data as well as the differences between the segments.

Figures 27 and 28 for the southern Lake Huron epilimnium show a seasonal pattern, especially in 1974 for which there is both CCIW and GLRD data. At this level of aggregation the comparisons between the two different data sets are quite reasonable and they compliment each other nicely. The general trends are apparent and consistent with expected seasonal patterns: lower nutrient concentrations and secchi depths as the plankton population develops, with the recovery of nutrient concentrations after the fall overturn. Zooplankton biomass data, however, is quite variable between the two years as is C^{14} primary production. Differing techniques are the probable cause, although the data does set the range for these variables.

Figures 30-31 for Saginaw Bay show much more marked seasonal patterns but again no marked difference between the two years (the CCIW soluble reactive phosphorus for 1971 appears suspect). CCIW and CIS data are comparable for 1974 with the increased temporal and spatial coverage clearly delineating the seasonal features: a bimodal chlorophyll distribution, sustained nitrate uptake, fairly constant total phosphorus concentrations, a marked silica uptake during the spring diatom bloom with a recovery during the summer and fall and an essentially constant secchi depth during the ice-free period.

Hypolimnion data for the northern and southern lake segment show practically constant values for nearly all variables and no differences between the two years. A seasonal pattern for soluble reactive and total dissolved phosphorus is suggested by the data which, when combined with the chlorophyll data for southern Lake Huron suggested seasonal algal activity in these deep waters. This feature of the data will be discussed subsequently in light of the model calculations for these segments.

The similarity of the two years data in the large main lake segments is to some extent expected since the hydraulic detention times of the lake is in excess of twenty years and differences in mass loadings, if they existed, would not appreciably change the concentrations over the three year period between the two sets of observations. For these comparisons it is clear that the 1974 data set is comprehensive and well suited for an analysis based on the kinetics and transport discussed in the previous sections.

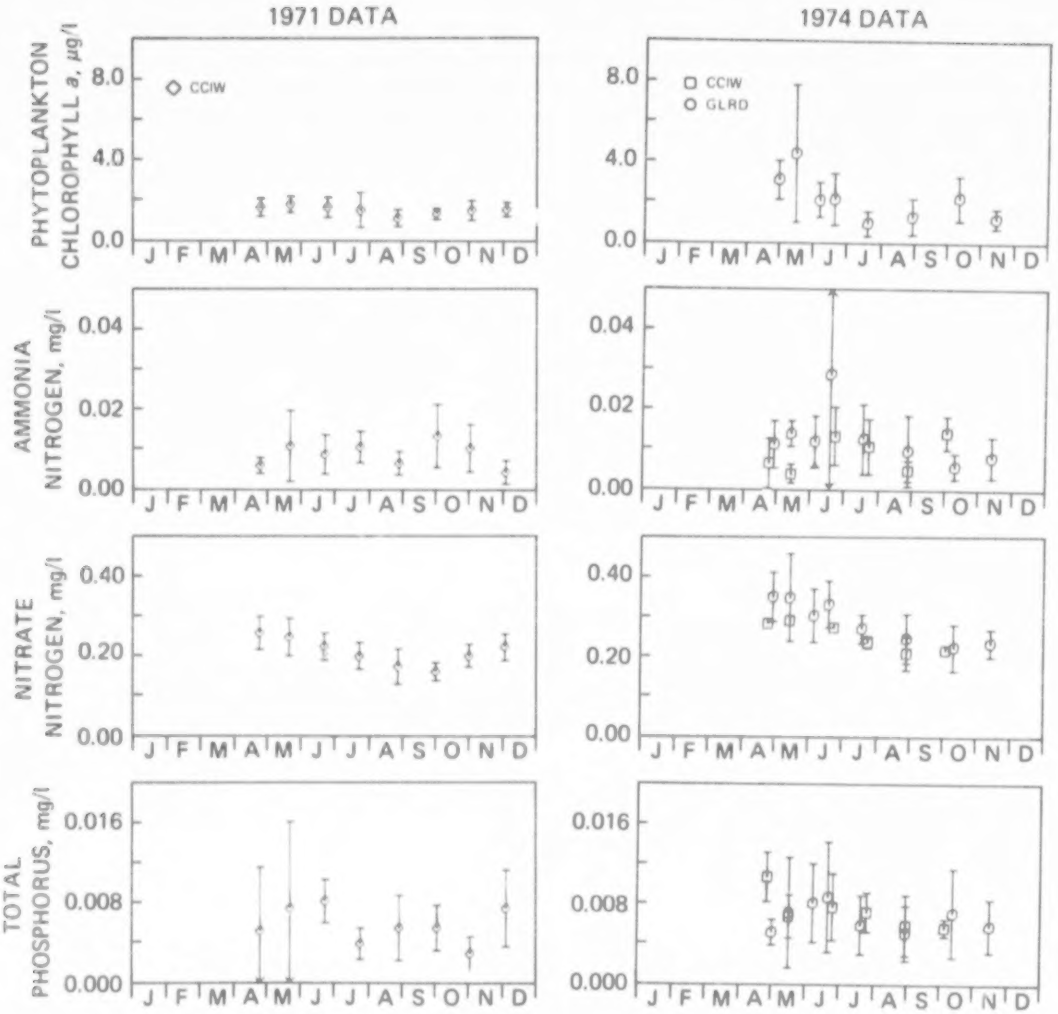


Figure 27. Model Calibration Data (Segment 2)

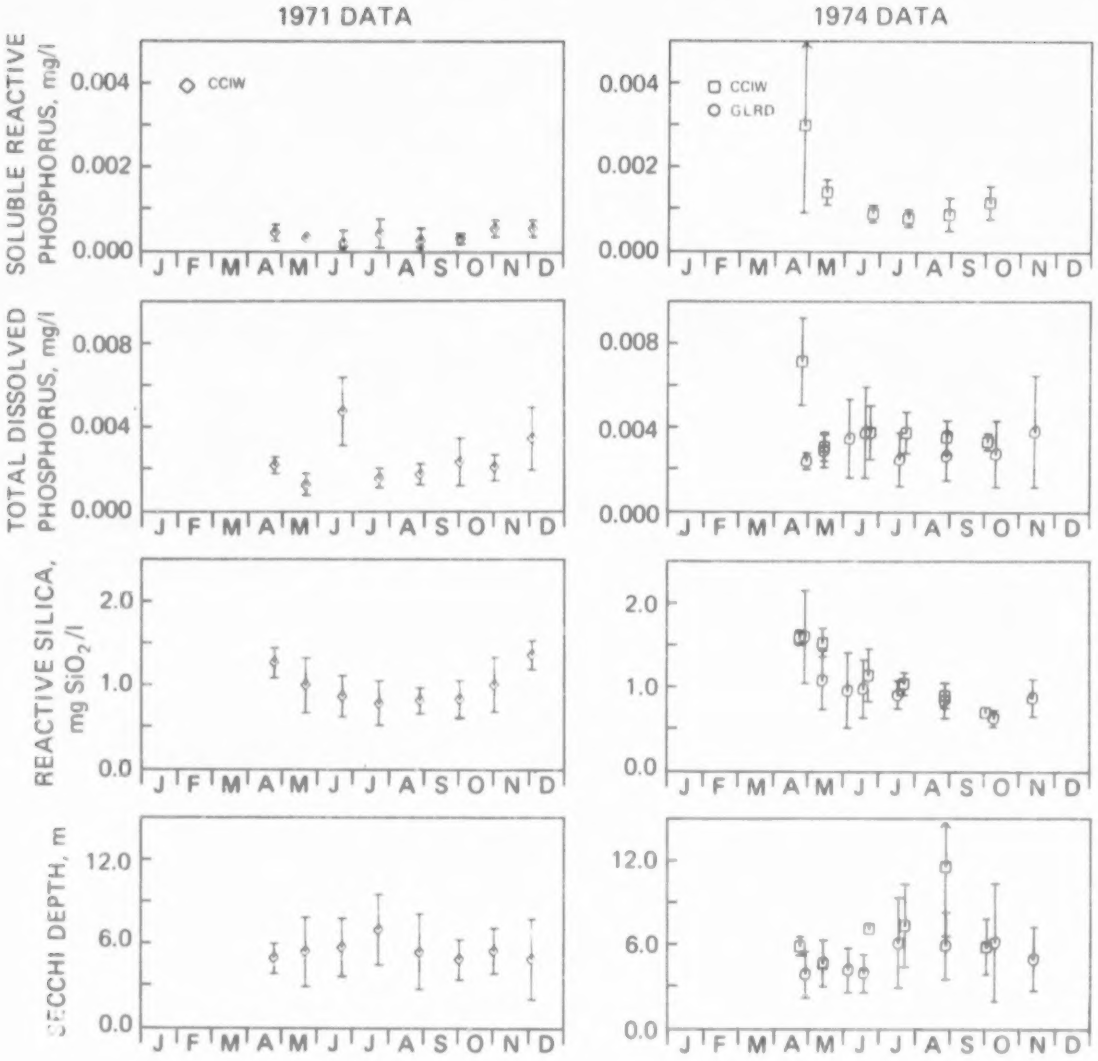


Figure 28. Model Calibration Data (Segment 2)

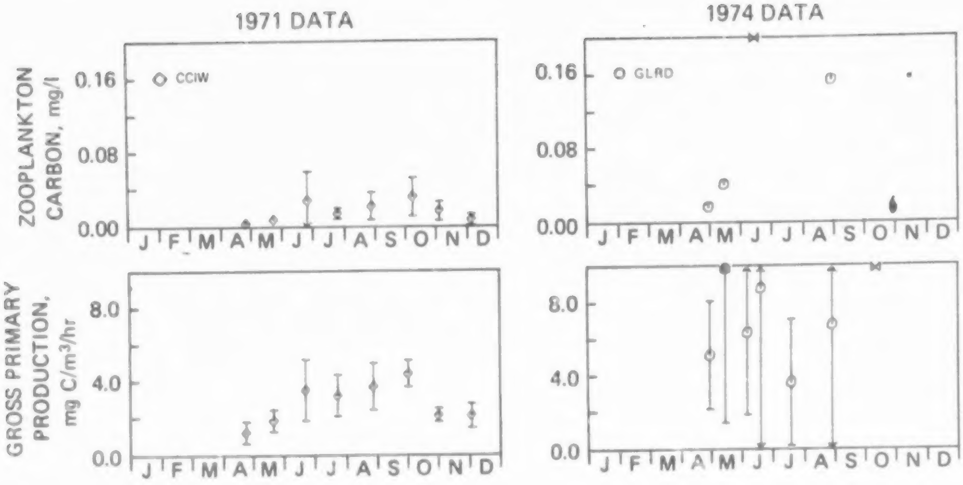


Figure 29. Model Calibration Data (Segment 2)

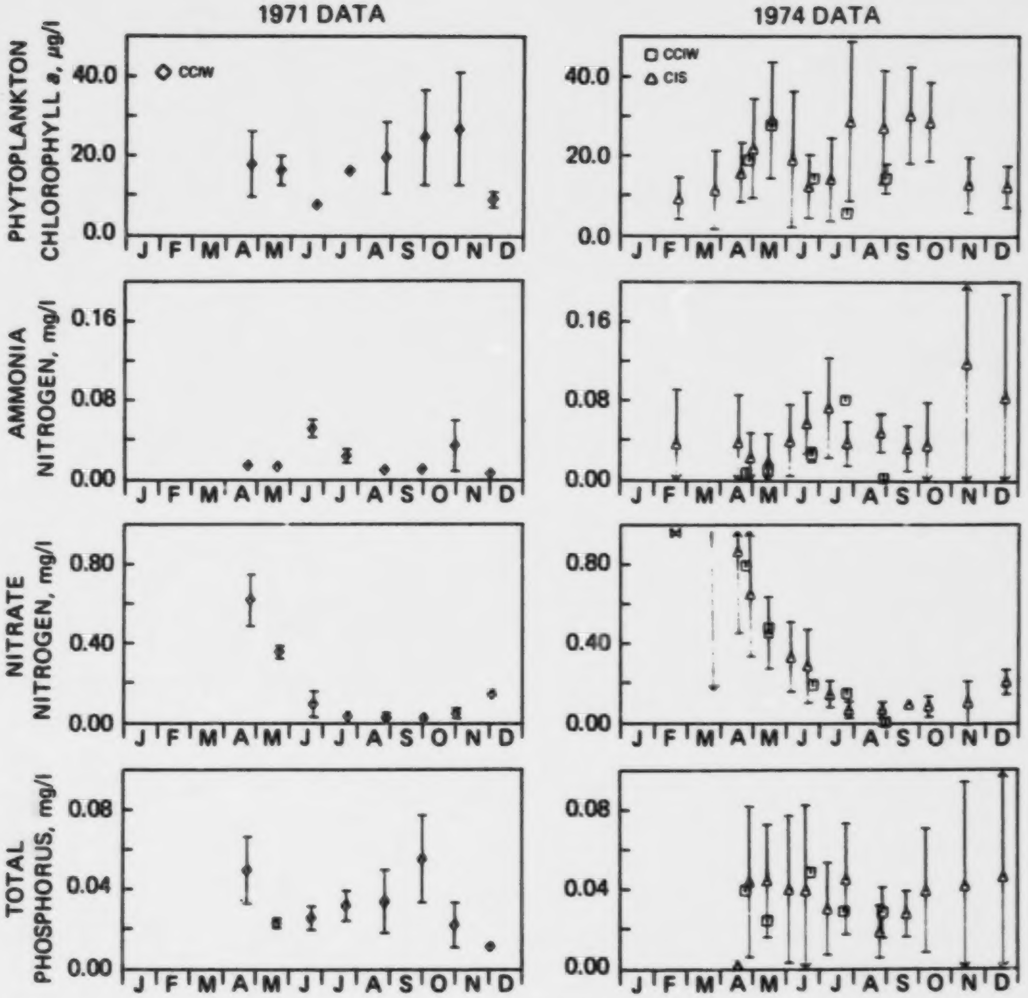


Figure 30. Model Calibration Data (Segment 3)

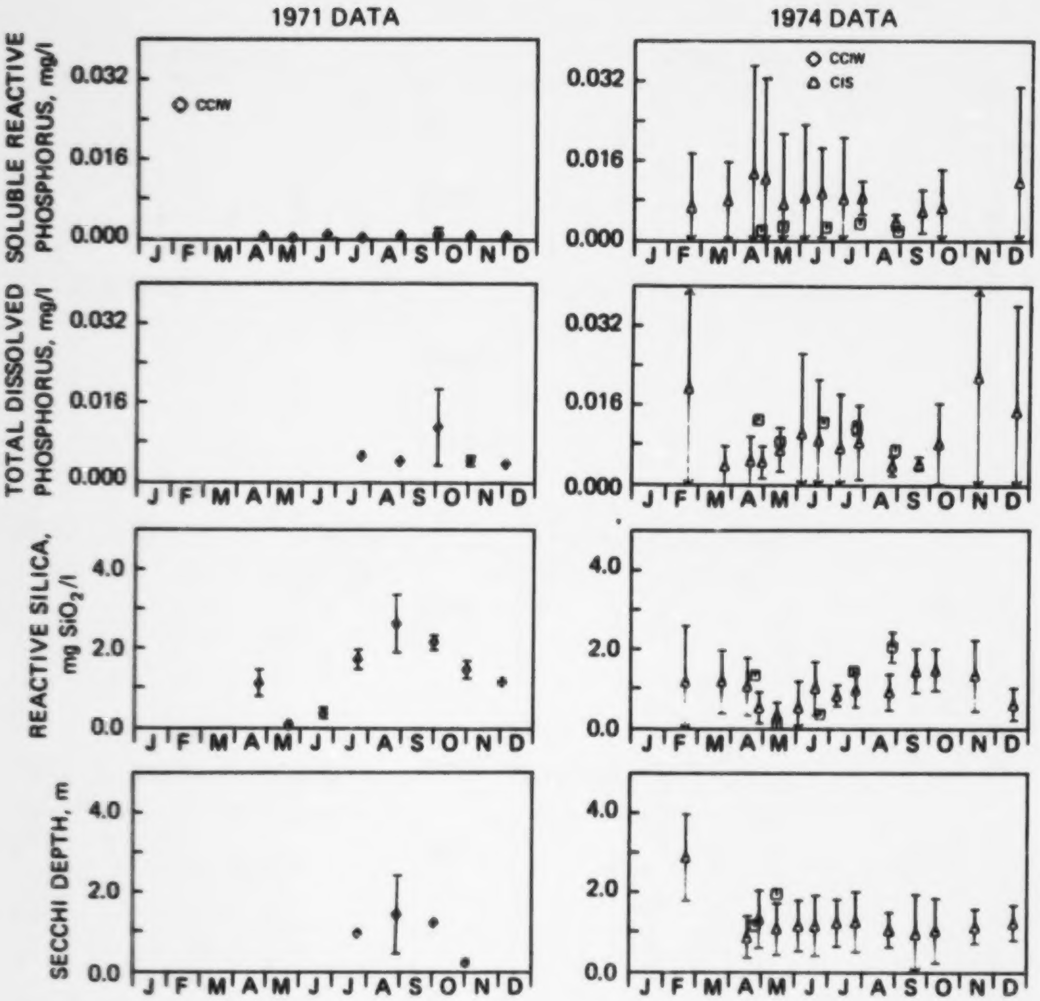


Figure 31. Model Calibration Data (Segment 3)

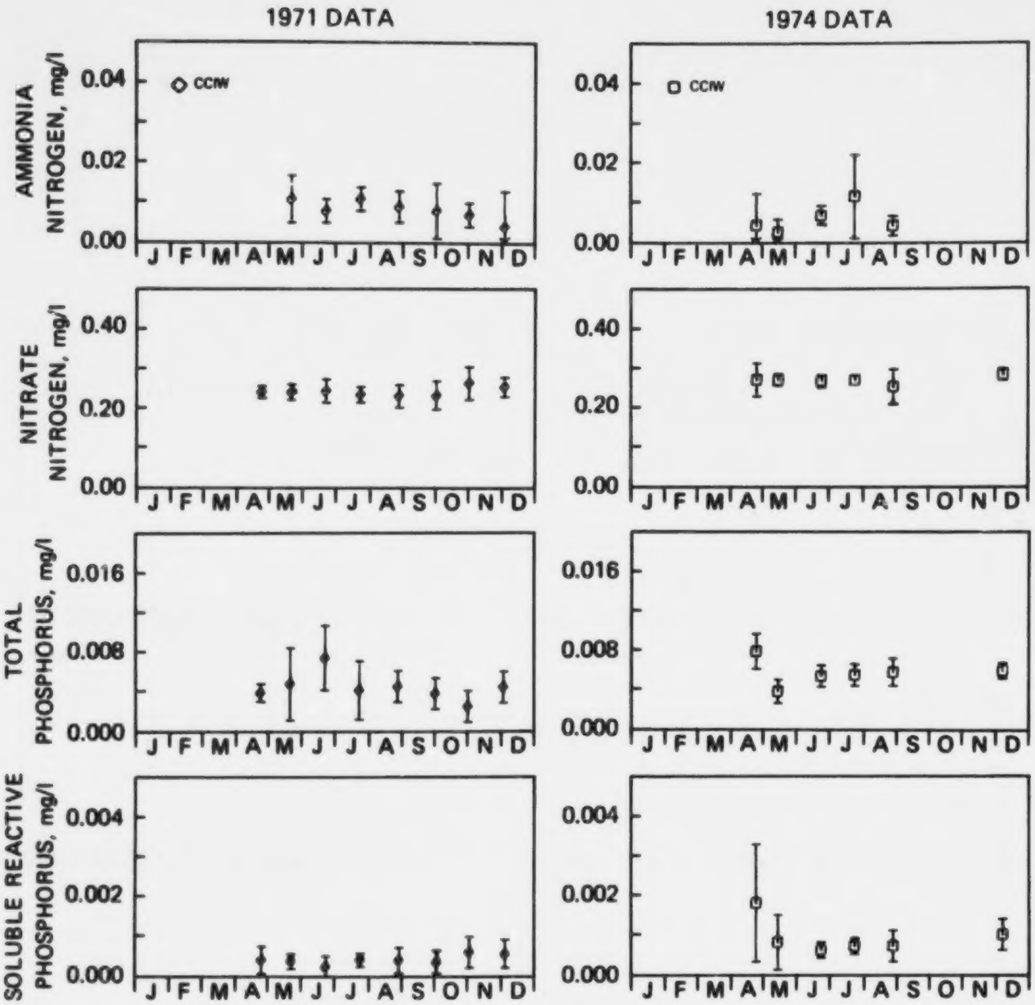


Figure 32. Model Calibration Data (Segment 4)

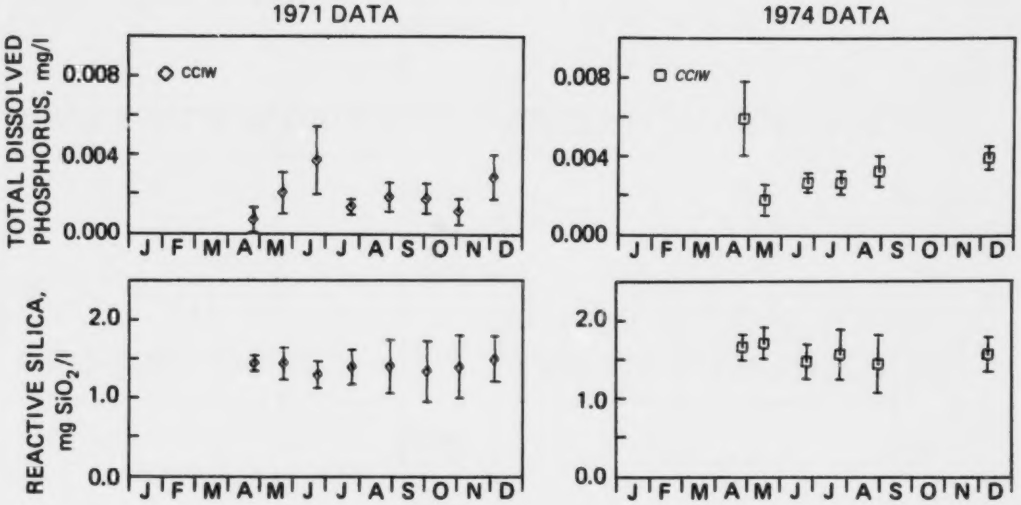


Figure 33. Model Calibration Data (Segment 4)

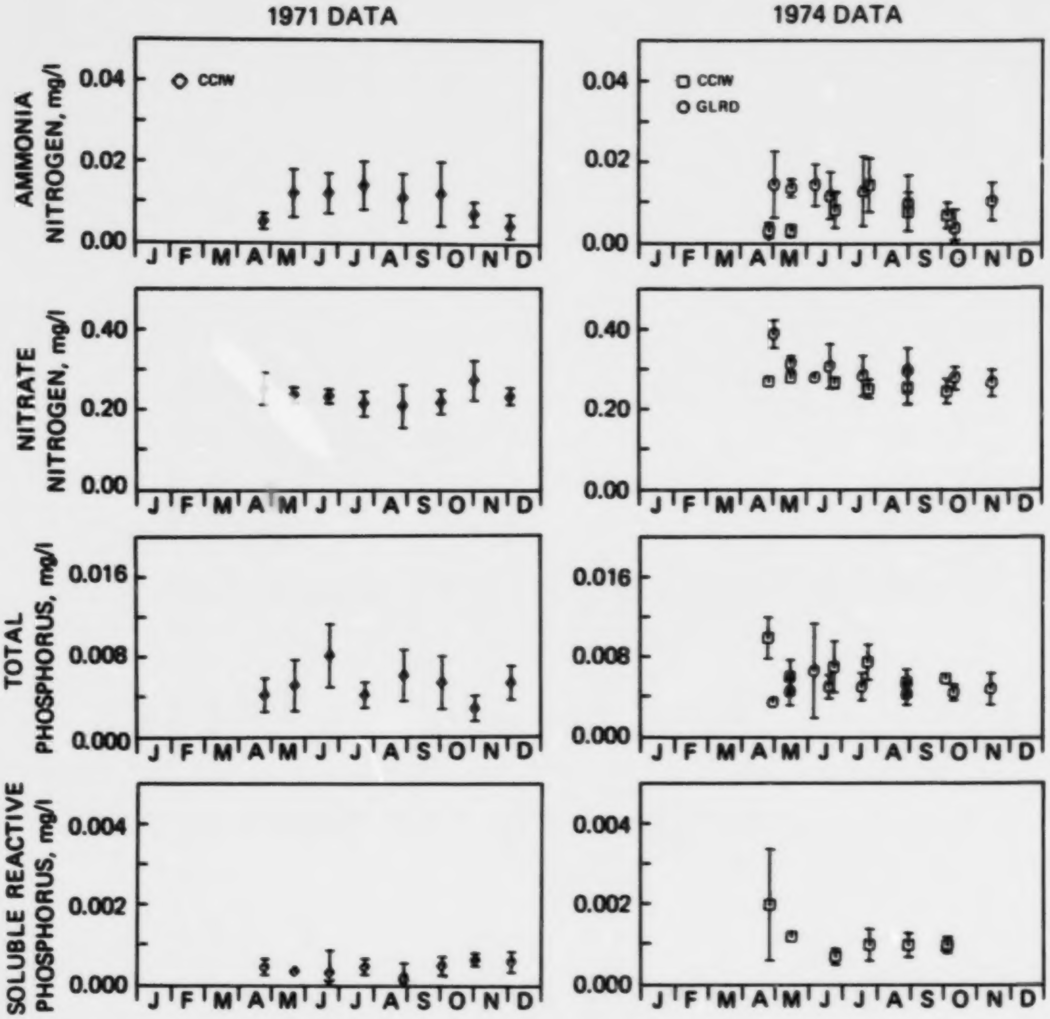


Figure 34. Model Calibration Data (Segment 5)

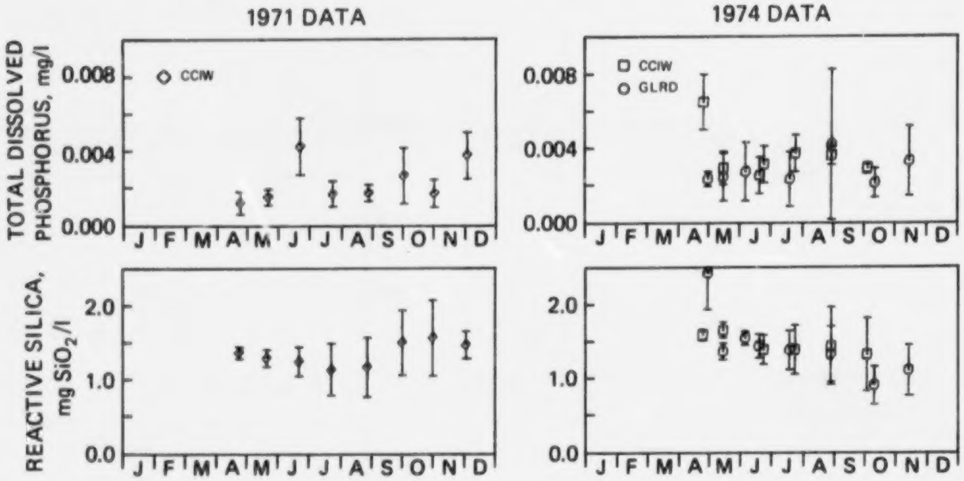


Figure 35. Model Calibration Data (Segment 5)

SECTION 8

MODEL STRUCTURE AND CALIBRATION

In the preceding sections the necessary components of the eutrophication model have been discussed: the transport between the segments; the mass loadings to the segments; and the kinetics within the segments. It remains to combine these elements into a consistent set of equations and to estimate the values of certain kinetic coefficients by calibrating the model against the data set described in section 7.

MODEL STRUCTURE

The variables included in the model calculations are dictated primarily by two facts: the available data, and their importance as either variables of concern, e.g. phytoplankton chlorophyll, or as a component of the kinetics, e.g. unavailable phosphorus. The eight dependent variables of the calculations are shown in fig. 36. The phytoplankton biomass that develops in a body of water depends on the interactions of the transport to which they are subjected and the kinetics of growth, death, and recycling. Phytoplankton biomass growth kinetics are a function of water temperature, incident-available solar radiation, and nutrient concentrations, specifically inorganic nitrogen and phosphorus. Phytoplankton also endogenously respire and are predated by herbivorous zooplankton which grow as a consequence. They, in turn, are predated by carnivorous zooplankton whose biomass also increases. Zooplankton grazing and assimilation rates are functions of temperature and, for the herbivorous zooplankton, the phytoplankton biomass as well. Zooplankton respiration is temperature dependent. The nutrients, which result from phytoplankton and zooplankton respiration and excretion, recycle from unavailable particulate and soluble organic forms to inorganic forms, ammonia and orthophosphate for nitrogen and phosphorus respectively. The recycle kinetics are temperature dependent and the rate is also influenced by the algal biomass present as discussed previously.

The spatial scale of the computation approaches a whole lake scale with the northern and southern regions of the lake, and the epilimnion and hypolimnion, differentiated. Saginaw Bay is also explicitly included. The time scale chosen for the calculation, which characterizes the main features of phytoplankton growth, is seasonal: the spring growing season during which the plankton utilize and are eventually limited by available nutrients as well as zooplankton grazing; the summer minimum; the secondary period of growth due to the fall overturn and/or nutrient regeneration and finally the winter decline. Variations of the environmental parameters on a time scale of less than bi-weekly are not considered. Thus although it is known, for example, that phytoplankton exhibit diurnal variations, such variations are

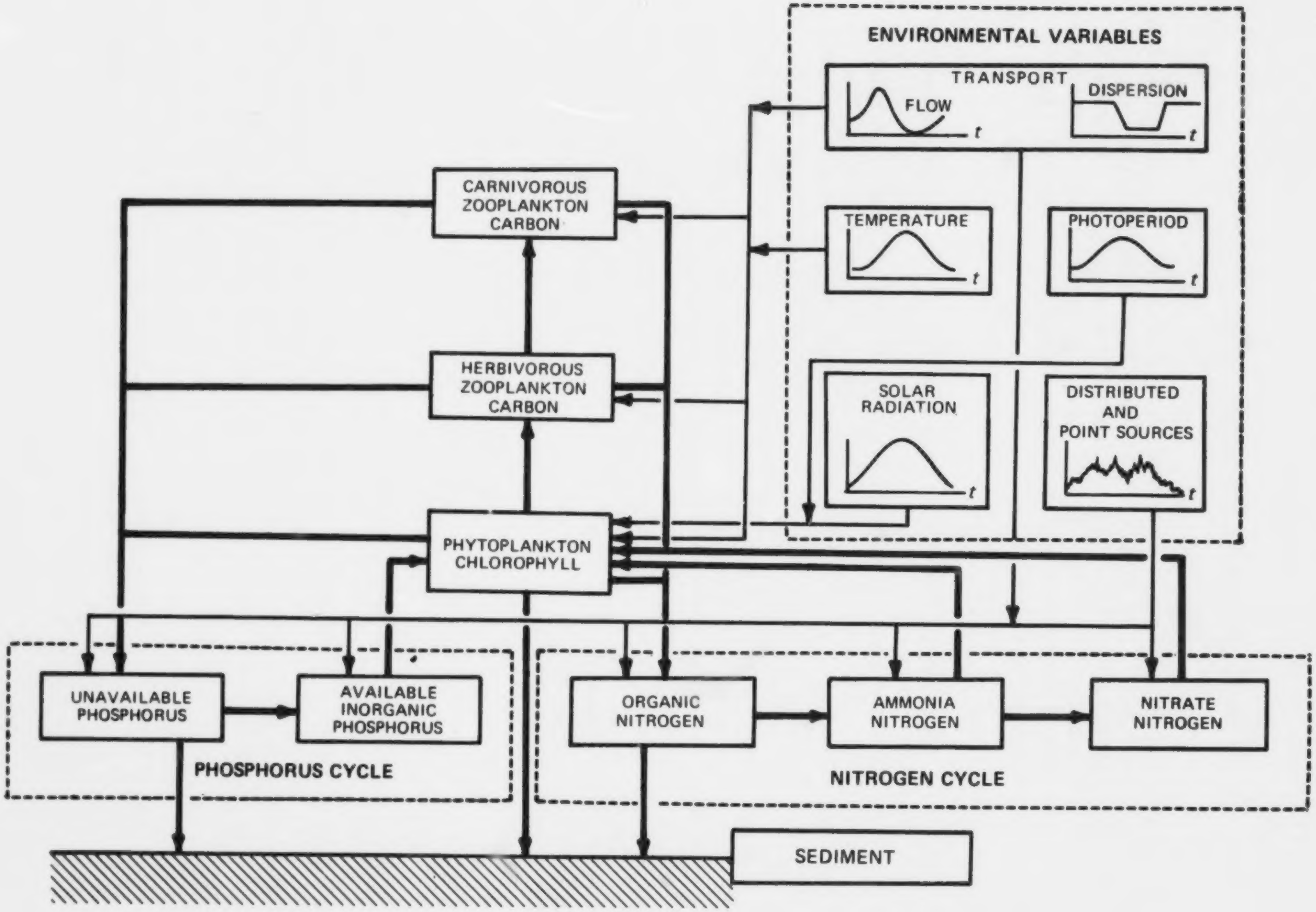

ENVIRONMENTAL VARIABLES
TRANSPORT
FLOW
t
DISPERSION
t
TEMPERATURE
t
PHOTOPERIOD
t
SOLAR RADIATION
t
DISTRIBUTED AND POINT SOURCES
t
CARNIVOROUS ZOOPLANKTON CARBON
HERBIVOROUS ZOOPLANKTON CARBON
PHYTOPLANKTON CHLOROPHYLL
UNAVAILABLE PHOSPHORUS
AVAILABLE INORGANIC PHOSPHORUS
PHOSPHORUS CYCLE
ORGANIC NITROGEN
AMMONIA NITROGEN
NITRATE NITROGEN
NITROGEN CYCLE
SEDIMENT

Figure 36. Schematic diagram of the kinetic iteractions incorporated in the eutrophication model structure.

not characterized in this calculation.

The numerical aspects are straightforward: it is time variable computation and uses a finite difference scheme to solve the differential equations by explicit forward time differencing. A time step of 0.5 days is used. The model has eight dependent variables or systems and five segments, which comprise 45 comprtments, a compartment being equivalent to one differential equation, which must be solved simultaneously. The computational burden is not excessive; it requires ∿ 22 central processer unit (CPU) seconds of CDC 6600 computer execution time for a one year model simulation. Additional peripheral processing approximately doubles the above figure. These figures include rather complete graphical displays of the results.

A complete presentation of the equations, the coefficients, and the forcing functions, boundary and initial conditions used in the subsequent calculations are presented in Appendix I. This is a complete specification of the model developed during this project.

MODEL CALIBRATION

The calibration is begun by assigning estimates of the coefficients which govern the kinetics based on field and/or laboratory information as well as prior studies. Successive adjustments of the coefficients are made until reasonable agreement is achieved between computed results and observed conditions. This process is critical to a modeling effort. It is not enough that governing equations are written and solved. The results must be compared with observed conditions for all variables in all model segments. Only then can any degree of confidence be assigned to the results.

As shown in Section 7, Lake Huron and Saginaw Bay waters differ by more than an order of magnitude in some biological and chemical parameters. Thus the model must simultaneously reproduce the conditions in a locally eutrophic area as well as large oligotrophic areas. This section contains a discussion of the problems encountered in attempting this calibration over an order of magnitude in the variables, the basis for incorporation of kinetic effects outlined in section 6, and insights gained during calibration procedure.

Recycle Rate

Early in the process, it became clear that phosphorus availability was a focal point of the analysis. Figure 37 illustrates the problem. In fig. 37(a) a relatively low first order recycle rate for unavailable phosphorus ($K' = .0084\ day^{-1}$) results in computed chlorophyll concentrations which match observed concentrations of phosphorus and chlorophyll fairly well in southern Lake Huron but not in Saginaw Bay. The observed peak concentrations in the bay are not reproduced, and the computed fall profile is substantially below the data. That this is due to low inorganic phosphorus availability is suggested by the fact that the effect is most apparent in the fall when recycling provides the major source of available nutrients due to low mass loadings during this period (fig. 8). The available phosphorus pool, replenished by recycle in mid-June, is rapidly depleted as a fall peak forms, thereby limiting further growth.

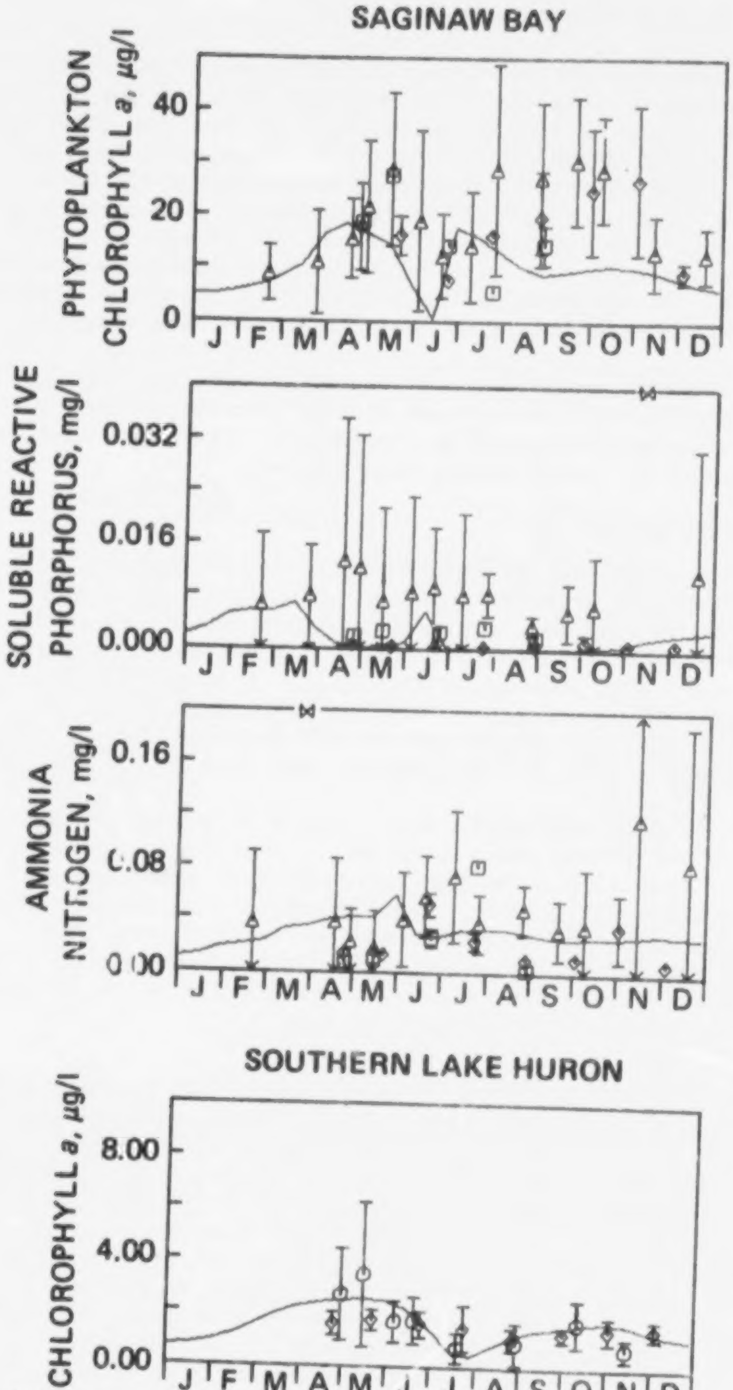


Figure 37. Calibration calculation for a recycle rate characteristic of Southern Lake Huron (bottom figure). Saginaw Bay chlorophyll and nutrients comparison (top three figures).

Figure 38 illustrates the opposite case. Using a relatively high first order recycle rate ($K' = .031\ \mathrm{day}^{-1}$), the computed chlorophyll concentrations match observed values in Saginaw Bay but are much too high in southern Lake Huron. Inorganic nutrient concentrations, especially soluble reactive phosphorus during the beginning and towards the end of the year are also high in comparison to observed values, indicating too rapid recycling of phosphorus. Note that the late fall and winter observations of soluble reactive phosphorus are critically important in determining the recycle rates.

A number of alternate hypotheses were examined in order to account for this discrepancy. For example at the low recycle rate Saginaw Bay chlorophyll is computed to be lower than observed. It might be possible that the transport across the Saginaw Bay-Lake Huron boundary is too large and the plankton are being flushed out too rapidly. Although the magnitude of the exchanging flow is set by the transport analysis based on conservative tracers (as described in section 5), it is possible that the phytoplankton calculation is more sensitive to this exchange rate than the conservative tracer calculation. The results, using the low first order recycle rate ($K' = .0084\ \mathrm{day}^{-1}$) which is suitable for southern Lake Huron, and with no exchanging flow between the bay and open lake, are that computed chlorophyll concentrations are comparable to observed magnitudes but computed total phosphorus and Kjeldahl nitrogen concentrations are more than double observed values (fig. 39). The chlorides and temperature calculations would also exhibit the same lack of agreement with observations. Thus inaccurate basin-lake exchanges are not the source of the problem.

Other possible hypotheses were investigated. For example, as shown in section 6, eq. (56), the phosphorus to chlorophyll ratio, a_{pP}, is important in determining the quantity of total phosphorus that is assimilated and becomes algal chlorophyll. However if it is varying it would be expected that the ratio is larger in Saginaw Bay where the quantity of inorganic phosphorus is larger than in Lake Huron. But this just compounds the difficulty since, as shown by eq. (56), and the sensitivity calculations in section 9, this would lower the computed chlorophyll in Saginaw Bay which is contrary to the direction required if the low recycle rate that appears reasonable for Lake Huron is used. Thus the conclusion that the recylce rate is different in these two regions becomes inescapable.

One possible solution to this dilemma would be to assign a different recycle rate to each segment. This, however, defeats the purpose of the calculations which are ultimately to be used to evaluate the effects of changes in mass loadings. For example if the loadings to Saginaw Bay were lowered substantially, with the high degree of mixing between the bay and the lake, Saginaw Bay would approach concentrations similar to those in the open lake waters. Then areas of similar properties would have different recycle rates since the rate had been assigned by segment. Similarly, if the mass loadings to the open lake waters of Lake Huron were increased to such a degree as to approach concentrations existing in Saginaw Bay, the model would have an unrealistically low recycle rate in these segments.

The fundamental problem with specifying site-specific kinetic constants

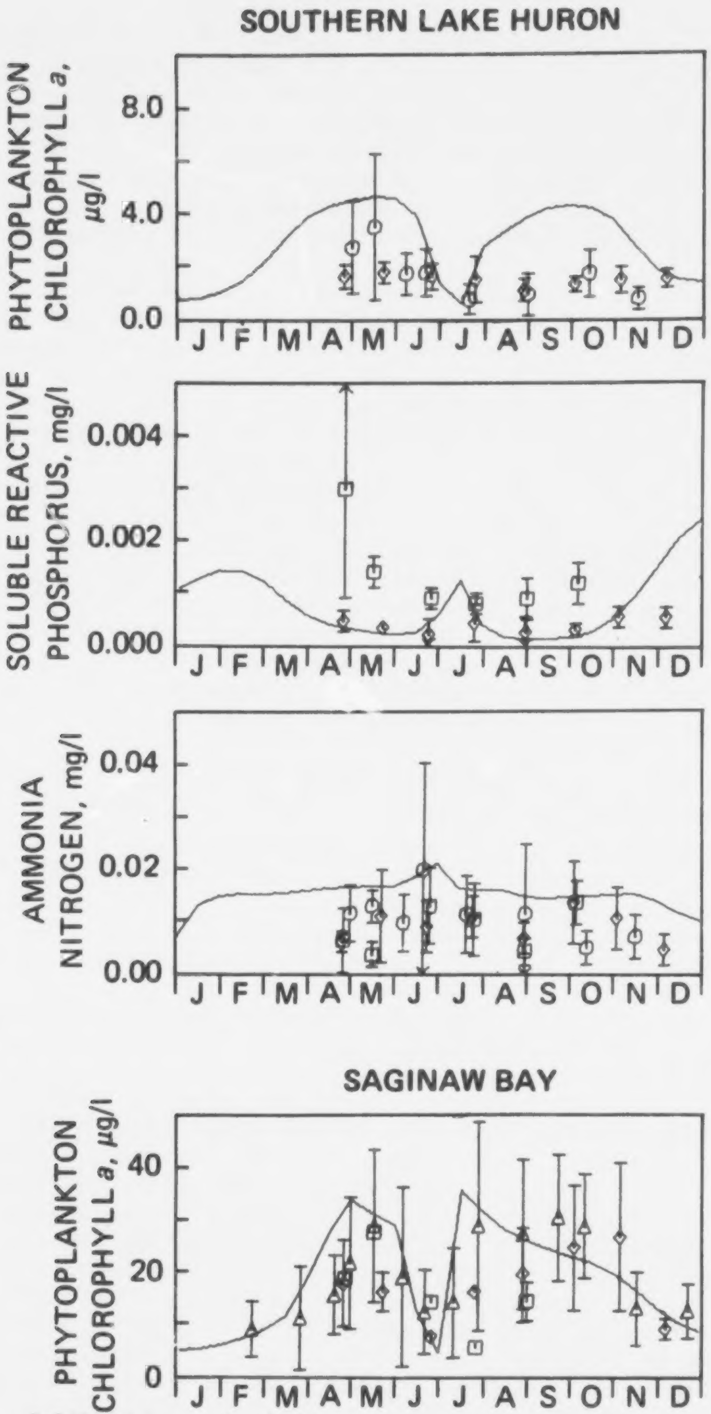


Figure 38. Calibration calculation for a recycle rate characteristic of Saginaw Bay (bottom figure). Southern Lake Huron chlorophyll and nutrients comparison (top three figures)

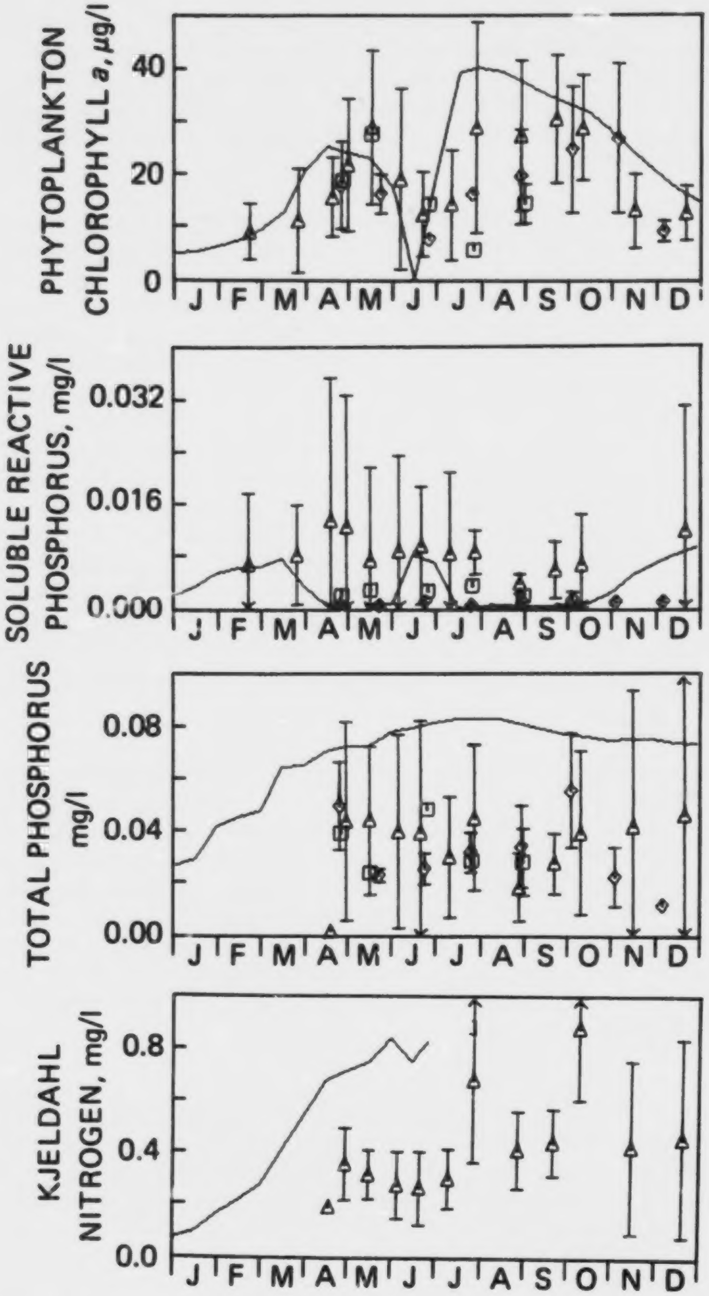


Figure 39. Calibration calculation for a recycle rate characteristic of Southern Lake Huron. Saginaw Bay-Southern Lake Huron transport exchange rate set to zero.

is that it defeats the purpose of the kinetic formulation, which is to properly characterize processes, independent of the particular geographical location in which they are occurring. The more site-specific the kinetic constants are, the less realistic is the modeling framework since the model is being calibrated to one particular situation, rather than to the class of situations to which it is designed to apply. This theme is returned to subsequently in the discussion of the application of the modified recycle kinetics to Lake Ontario.

The varying recycle rates are accounted for in the present calculation by relating the recycle rate to the chlorophyll concentration. At higher chlorophyll concentrations the recycle rate increases up to a limit that is consistent with observed laboratory rates. As shown in section 6, the available data from various regions in the Great Lakes supports this hypothesis. Saginaw Bay with its higher chlorophyll concentrations would therefore have a higher recycle rate and the inorganic phosphorus available for growth would be resupplied more quickly thus supporting a larger population. It should be noted that the same hypothesis is applied to the recycle of nitrogen and, since the recycle mechanisms are assumed to be the same as for phosphorus, the same rates are used. Initial calculations with the nutrient recycle rate directly proportional to phytoplankton concentrations (i.e. a second order recycle rate) indicated that this mechanism would provide the inorganic nutrient flux necessary to support observed growth in Saginaw Bay. Subsequent investigations described in the kinetics section (6) indicates that the recycle rate saturates with respect to chlorophyll concentration, and the calculations presented subsequently incorporate this formulation.

Zooplankton Kinetics

As discussed in section 6, the two mechanisms incorporated in zooplankton growth expression are a reduction in filtering rate and in assimilation efficiency as chlorophyll concentrations increase. Whereas the formulation for Lake Ontario included only assimilation efficiency decreases it was found that the same grazing rate did not apply to both Saginaw Bay and Lake Huron. A rate suitable for Lake Huron was invariably too large for Saginaw Bay. As soon as the spring bloom began in Saginaw Bay, herbivorous zooplankton growth would increase to such an extent that they would exert too much grazing pressure on the phytoplankton, reducing their concentrations to below observed peak values.

Perhaps this effect appeared so dramatically in the Saginaw Bay-Lake Huron calculations because of the order of magnitude difference in chlorophyll concentrations in the two regions. Zooplankton grazing at the high rates required to produce the observed population biomass in Lake Huron, would overgraze the Saginaw Bay population. The modification to the zooplankton feeding expression which reduces the grazing coefficient as chlorophyll increases is an attempt to parameterize this effect. Whether the effect is physiologically actually taking place, or whether this is just a method of computationally accounting for the different species of zooplankton in the very different regions awaits further investigation.

Primary Production

Primary production investigations of Lake Huron and Saginaw Bay are available [91] and provide additional supporting data for the calibration. Both in situ and shipboard measurements can be used for comparisons to calculations. The relevant expressions are directly available from the kinetic equations for biomass growth. Since these assume that growth, carbon and other nutrient assimilations are simultaneous and, on the weekly time scale of the calculation this is reasonable, the in situ gross carbon assimilation rate is $a_{CP}G_P P$ where a_{CP} is the carbon/chlorophyll-a ratio of the biomass. For shipboard measurements the time and depth averaged light reduction factor is not appropriate so that the instantaneous rate reduction expression, eq. (26), evaluated at the light intensity of the incubator is used instead. The temperature and nutrient factors are assumed to be at their in situ values, which is consistent with the experimental procedure.

The primary production data are, therefore, direct measurements of a rate, and a critical rate, in the kinetic equation of phytoplankton growth. And, unlike all the other data which measure the quantities at the time and location of sampling, and from which rates are inferred via the calibration, the primary production gives an estimate of the assimilation rate directly. Further the primary production exhibits a thirty fold variation between Southern Lake Huron and Saginaw Bay. This large difference is a stringent test of the calculations since if the kinetics can reproduce these variations one's confidence in their validity increases.

Calibration Results

Figures 40 to 42 show the comparison of computed profiles to observed data for the northern Lake Huron epilimnion segment. For these and all subsequent calibration plots the data are cruise averages ± the standard deviation. Phytoplankton chlorophyll-a concentrations peak at approximately 2 μg/ℓ in early June, and are limited by the rate of phosphorus recycle. The decline to a mid-August minimum is due mainly to grazing pressure exerted by the herbivorous zooplankton. They in turn are grazed by the carnivors which develop a significant population commencing in early August leading to a decline in the herbivors and subsequent fall phytoplankton growth. Not quite enough fall phytoplankton growth is achieved, however, and it is apparently due to the combination of excess grazing, since the herbivors still maintain enough of a population to exert pressure throughout the fall, and perhaps to an underestimation of fall recycle rate. Ammonia concentrations are both computed and observed to be in the range of 5-10 μg N/ℓ. The low concentration is maintained by algal uptake and nitrification sinks. Available phosphorus is computed to be reduced to below the half saturation constant of 0.5 μg PO_4-P/ℓ which then severely limits growth. The abnormally high observations in April 1974 are unexplained and are not consistent with 1971 observations.

Nitrate nitrogen concentrations range between 0.2 and 0.3 μg N/ℓ as shown in fig. 35. The fall depression of nitrate is not reproduced by the calculation. It may represent a larger uptake of nitrate in the fall by a species with a larger nitrogen to chlorophyll ratio than the spring bloom

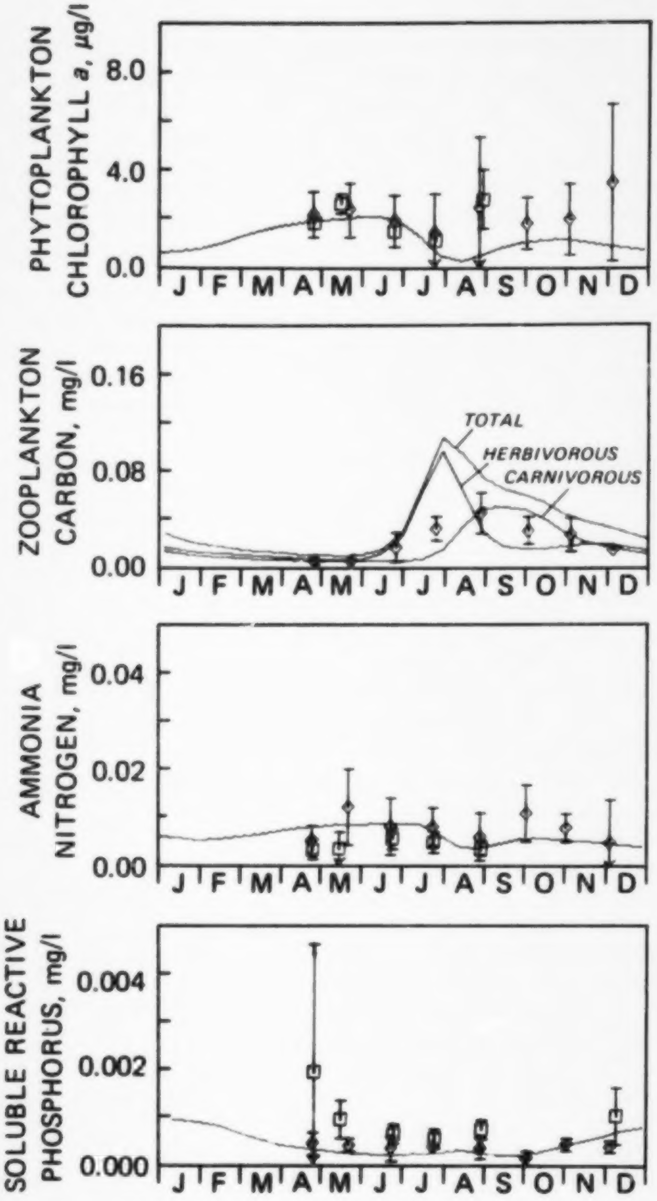


Figure 40. Northern Lake Huron Epilimnion Calibration Calculation. Comparison of observations and computations for phytoplankton chlorophyll, zooplankton carbon, ammonia nitrogen and soluble reactive phosphorus, 1974. See figure for data symbol legend.

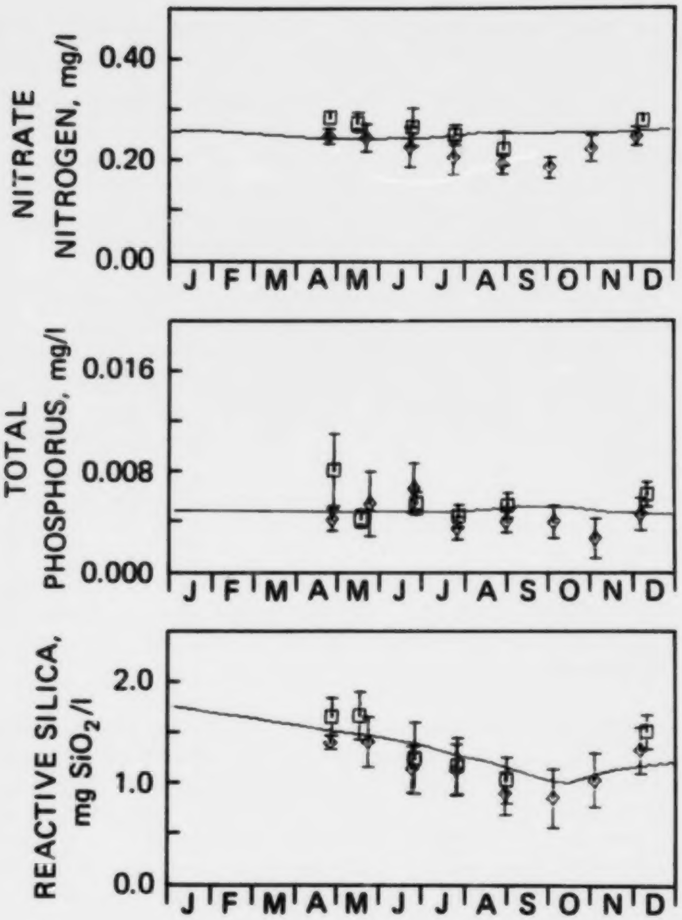


Figure 41. Northern Lake Huron Epilimnion Calibration Calculation. Comparison of observations and computations for nitrate nitrogen, total phosphorus, and reactive silica nitrate nitrogen total.

variety.

Total phosphorus concentration is calculated to remain essentially constant at 5 μg PO_4-P/ℓ throughout the year. Some seasonal variation is observed in the data, together with the high April 1974 observation. Variations in mass discharge rate cannot account for these fluctuations since the mass in the segment is much larger than the annual loading to the segment. Perhaps a transient settling of detrital particles into the hypolimnion during the latter part of the year is the cause, since an increase in unavailable phosphorus is calculated to occur during this period.

The reactive silica profile is computed by considering just silica uptake of the population. Since they are primarily diatoms a reasonable comparison is expected. The silica cycle is not included, however, and the computation is not meant to be representative of the actual recycle mechanisms. The reasonable agreement is taken to mean that over a one year period, the recycle source of silica is not critical at these concentrations. Note, however, that the computed curve is decreasing below the observations by year's end so that the effects of recycle would be very important for adequate multi-year calculations of silica.

Figure 42a compares computed and observed Secchi disk depth. The effect of increased chlorophyll during April through June in lowering the transparency and the increase due to reduced populations during July and August are in reasonable agreement with observations.

The comparison to observed primary production data is shown in fig. 42b. The data are for 1971 [91] in contrast to the other variables. However the comparison in section 7 of 1971 and 1974 data support the comparability of both these years. The computation overestimates the spring and underestimates the fall primary production. A smaller carbon to chlorophyll-a ratio is suggested by the spring data. With the discrepancies in the later part of the year related to the discrepancy in computed and observed chlorophyll. The final carbon to chlorophyll ratio is a compromise for both seasons.

The results for the southern Lake Huron epilimnion (segment 2), are shown in figures 43 to 45. Phytoplankton growth exhibits the same behavior as in northern Lake Huron epilimnion but both the computed and observed spring concentrations are slightly higher and in better agreement. Zooplankton growth is also similar and the fall peak is again limited by herbivore grazing and phosphorus limitation with nitrogen limitation not being a factor. Calculated zooplankton biomass concentrations exceed that estimated to be present based on the 1971 data but is lower than the 1974 estimates (see fig. 18) which are not included in this figure. The general state of both biomass estimates and the calculation is unsatisfactory. The uncertainty in both the observations and the relevant kinetic constants is sufficiently large so that the level of credibility of this portion of the calculation is uncertain and probably low.

Calculated ammonia nitrogen is within the range of the observations and is similar to the northern segment result. The available phosphorus calcula-

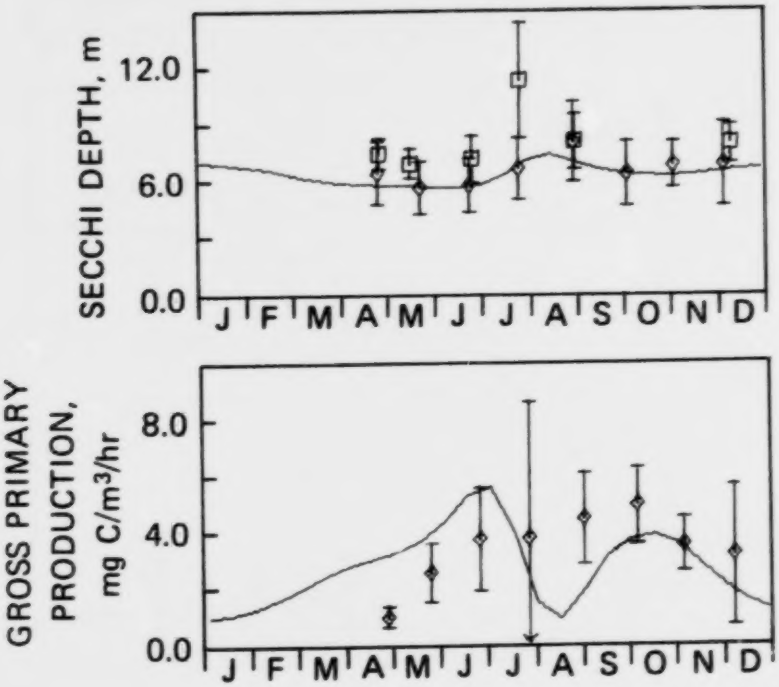


Figure 42. Northern Lake Huron Epilimnion Calibration Calculation. Comparison of observations and computation for observed Secchi disk depth and gross primary production, (1971).

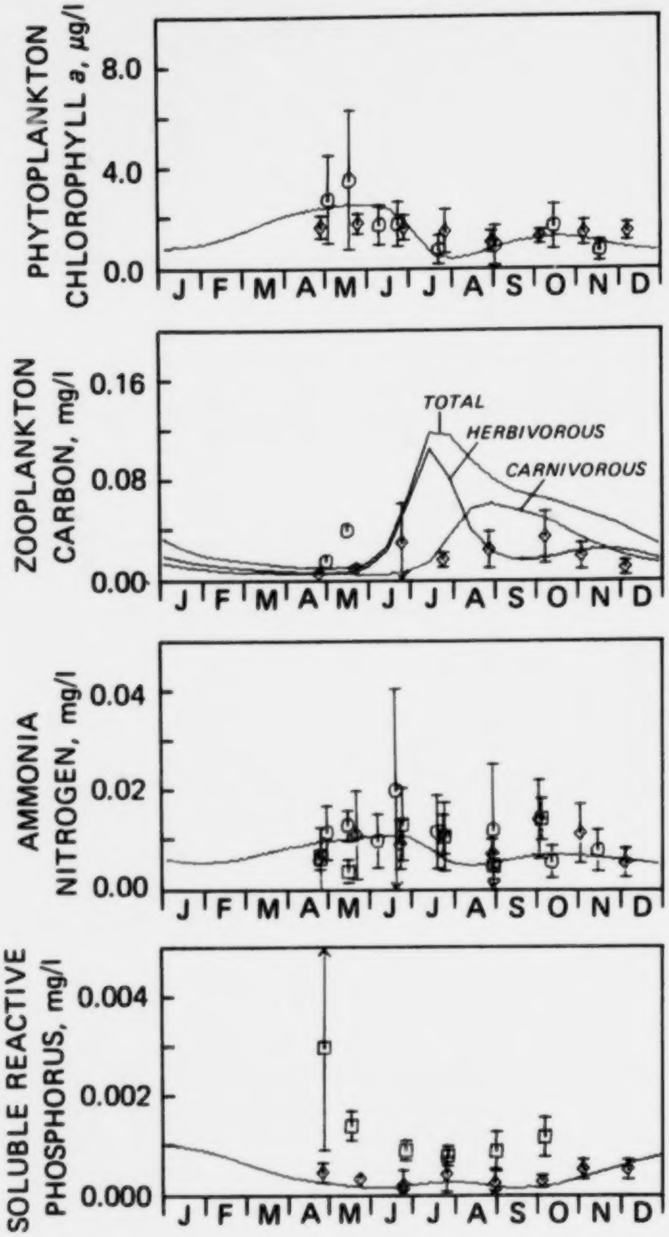


Figure 43. Computed versus Observed Data (So. Lake Huron epilimnion)

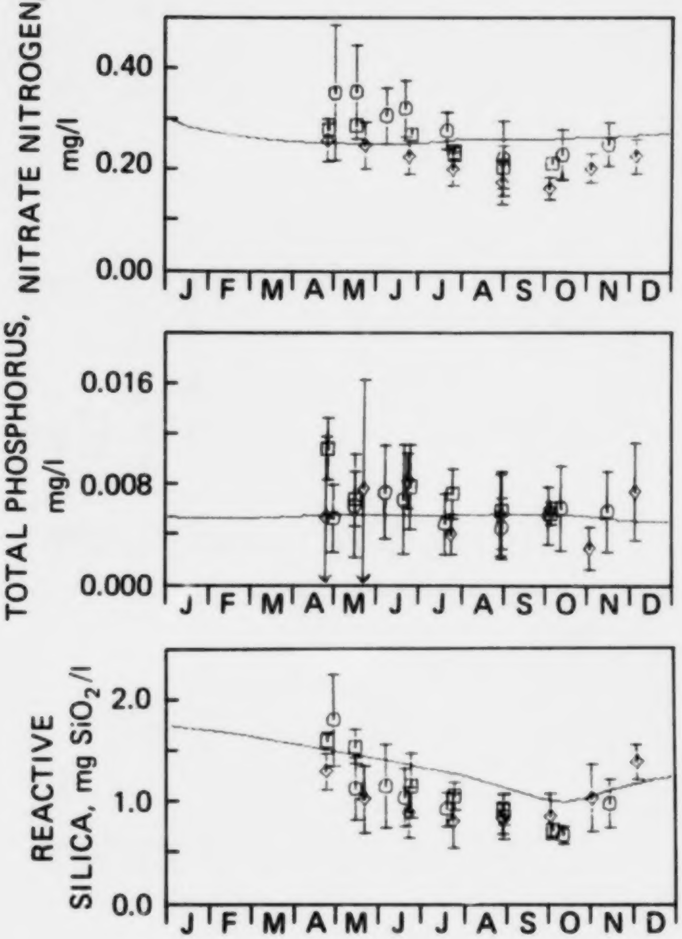


Figure 44. Computed versus Observed Data (So. Lake Huron epilimnion)

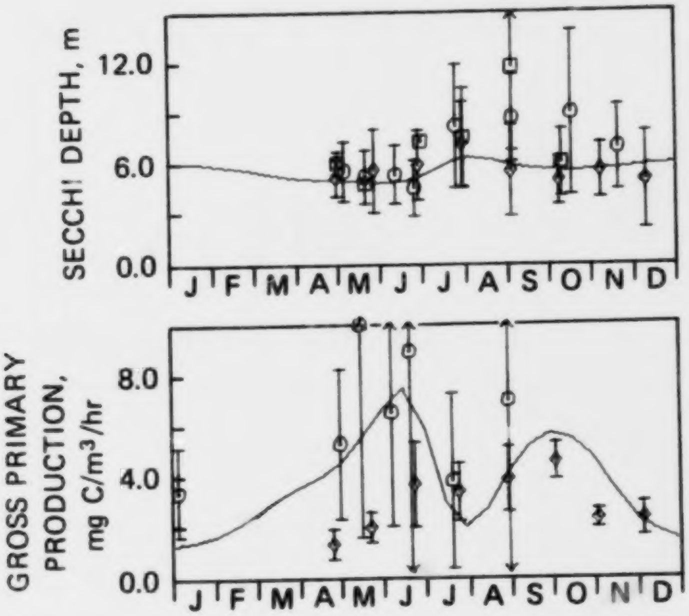


Figure 45. Computed versus Observed Data (So. Lake Huron epilimnion).

tion agrees with the observed 1971 data but not the substantially higher values observed in 1974. No ready explanation of this discrepancy is available. Nitrate nitrogen data again shows a fall depression which is not reproduced by the calculation. Total phosphorus data are somewhat erratic if all the data are overplotted as in this figure. The individual year's data as shown in fig. 27 do not appear to have any strong seasonal trends although there is a suggestion of a fall decrease as in the northern lake epilimnion data. The silica profile follows observed patterns although it appears that more uptake is required. Transparency as measured by Secchi depth, agrees well and computed gross primary production falls within the range of observed data for both 1971 CCIW data and 1974 GLRD data as shown in fig. 45.

The Saginaw Bay calculation is shown in figures 46 to 48. Notice the difference in plotting scales used for these computed profiles and observations to those used for the open lake segments presented above. Phytoplankton and reactive phosphorus concentrations are approximately 15 times greater, zooplankton populations are approximately 5 times higher, while inorganic nitrogen, ammonia and nitrate values are approximately 4 times higher than in the main lake segments. Thus Saginaw Bay spans almost an order of magnitude change in the concentration of most variables.

Both the data and the calculation show two peaks in Saginaw Bay phytoplankton with the spring pulse declining during the beginning of July. A broad fall peak extending through November is indicated by the data. The calculated concentrations taper off progressively in the fall with a significant population decline starting at the end of October. Fall growth limitation is due to both zooplankton grazing and phosphorus limitation. It can be seen on figure 47c that the calculated total phosphorus also is low at the end of the year. This suggests that a significant phosphorus source at the end of the year may not have been accounted for. This may be due to resuspension of sediment phosphorus or a mass discharge which eluded measurement.

Zooplankton biomass is reproduced quite well as can be seen in fig. 46b. The magnitude of a pulse at the end of July which limits phytoplankton growth is reproduced although the calculated biomass is slightly in excess of that observed in the fall. Computed ammonia concentrations are slightly high during the spring as are the Kjeldahl nitrogen calculations.

The problem may be due to an overestimation of the detrital nitrogen mass loading rate or increased settling of particulate nitrogen during the spring. Nitrate uptake as calculated and observed is shown in fig. 47a. The agreement is quite remarkable. Soluble reactive phosphorus data are quite variable although the calculation appears to be below the observations for significant portions of the spring.

Secchi disk observations are compared to calculations in fig. 48b. The small variations due to algal chlorophyll are not significant. The February measurement is through the ice cover and therefore is not representative of the total light available since the attenuation due to the ice is not measured. The primary production data for the summer and fall are well repro-

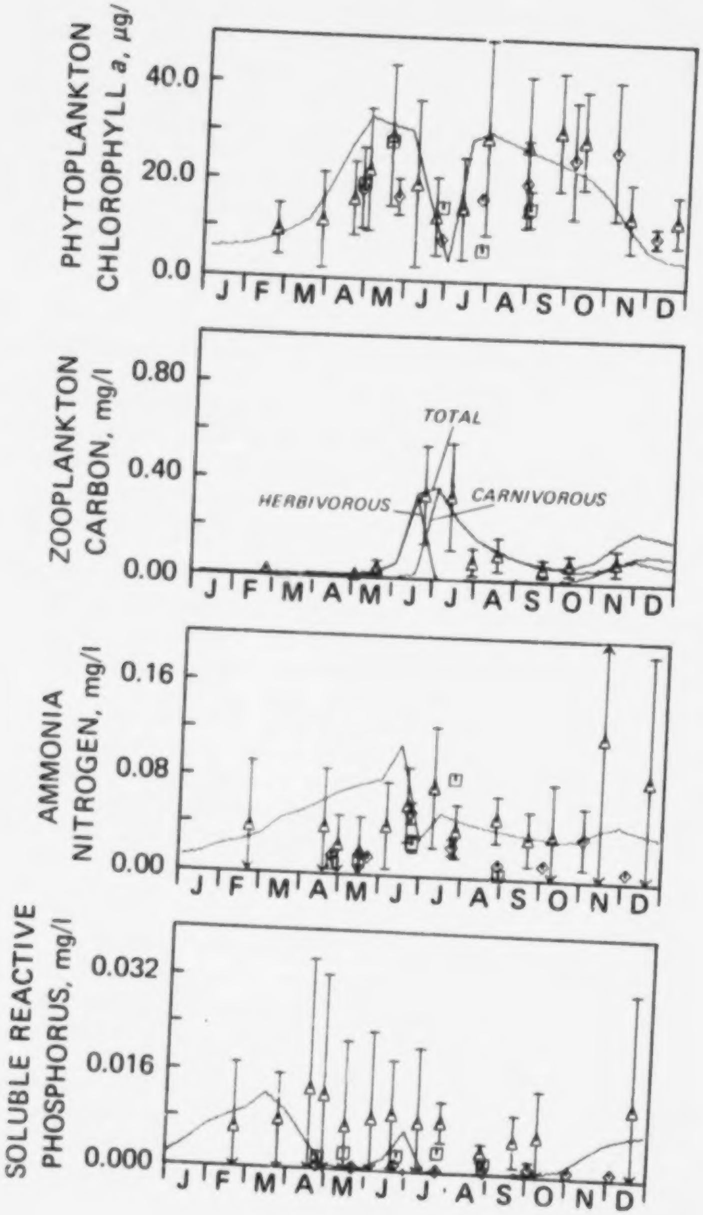


Figure 46. Computed versus Observed Data (Saginaw Bay)

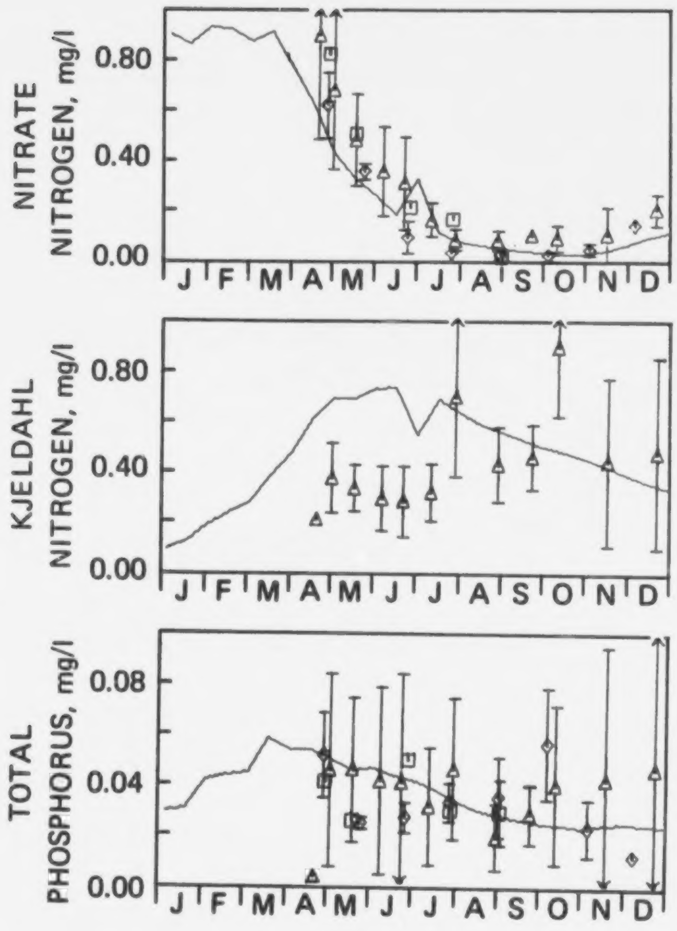


Figure 47. Computed versus Observed Data (Saginaw Bay)

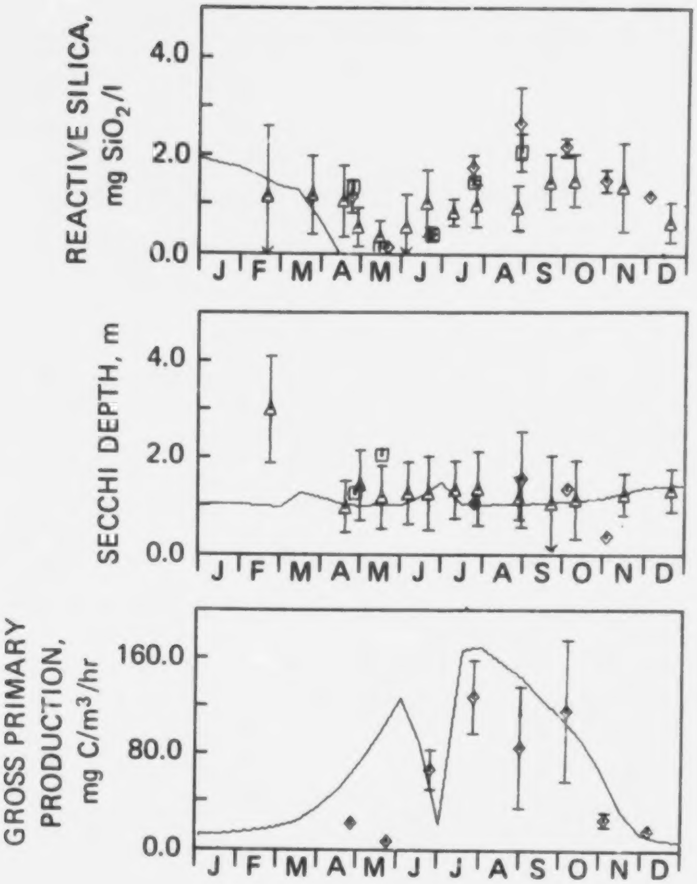


Figure 48. Computed versus Observed Data (Saginaw Bay)

duced. The low values observed in the spring during the height of the diatom bloom are unexplained and appear suspect.

The bottom layer segments representing the northern and scuthern lake hypolimnia are in reasonable agreement with observations. Figures 49 and 50 show the computed profiles compared to observations for the northern Lake Huron hypolimnion. No chlorophyll data for comparison are available as the CCIW measurements are integrated samples only in 1974 and surface concentrations in 1971. Calculated concentrations average only 0.3 μg/ℓ on a yearly basis due to light limitation as the hypolimnion is well below the euphotic zone. Computed profiles for the other variables agree reasonably well with observations.

The comparison of the computation and observed data for the southern Lake Huron hypolimnion is shown in figs. 51 and 52. In fig. 51a, it can be seen that the model calculates phytoplankton chlorophyll-a concentrations substantially lower than the observations by GLRD in 1974. Nitrate and reactive phosphorus concentrations agree reasonably well, so there are no nutrient limitation problems. Total inorganic nitrogen and available phosphorus are both well above their respective half saturation constants. The reason for the lower computed profile can be seen in fig. 53, which presents the phytoplankton growth rate which results after light and nutrient limitations are imposed on the saturated temperature dependent rate. The comparison shown is between the epilimnion and hypolimnion segments in the southern lake. It can be seen that in the epilimnion, light limitation accounts for a 30 to 80 percent decrease in the saturating rate with nutrient limitation also being significant. In the hypolimnion, however, light limitation amounts to greater than a 99.9% reduction in the saturating rate. Nutrient limitation is unimportant as is zooplankton grazing in comparison to light effects.

Based on the relationship developed by Beeton [17] from studies on Lake Huron, the extinction coefficient can be approximated as 1.9/Secchi depth. The epilimnion segment with an average Secchi depth of 6 meters has an extinction coefficient of .32 meter^{-1}, yielding an equivalent euphotic zone depth of approximately 15 meters. Thus less than 1% of the surface irradiation is available at a depth of 15 meters, the upper bound of the hypolimnion segment. This lack of available radiation causes the large computed reduction in the depth average growth rate in the hypolimnion. Since the computed respiration rate exceeds the computed growth rate as shown in fig. 53b, the phytoplankton kinetics are, on balance, causing a net loss of biomass. The slight increase calculated in the hypolimnion is due to vertical transport via mixing and settling from the epilimnion with the former predominating as shown subsequently.

The phenomenon of a significant standing crop of phytoplankton in the meta- and hypolimnetic layers has come to be termed as "deep chlorophyll" and has been observed in recent lake studies [96]. The kinetics, as presently structured, are unable to characterize this effect since they are based on the hypothesis that severe light limitation will result in minimal phytoplankton growth. If the deep chlorophyll phenomena are reasonably well verified by further observation, the kinetics may be adjusted to incorporate

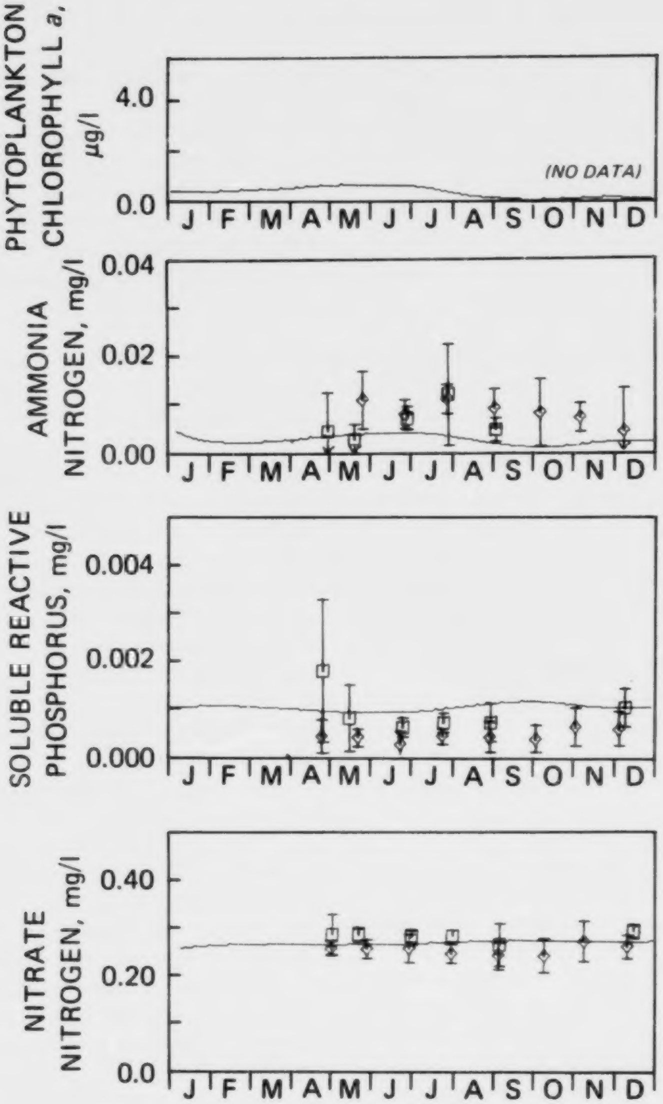


Figure 49. Computed versus Observed Data (No. Lake Huron hypolimnion)

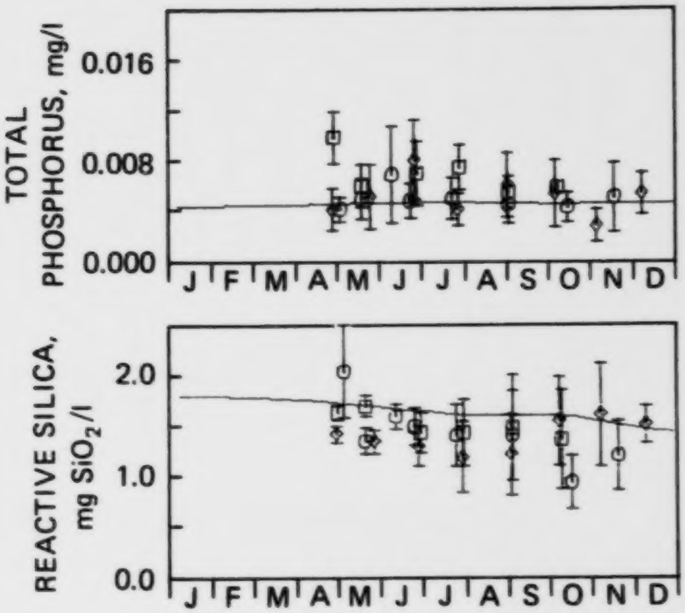


Figure 50. Computed versus Observed Data (No. Lake Huron)

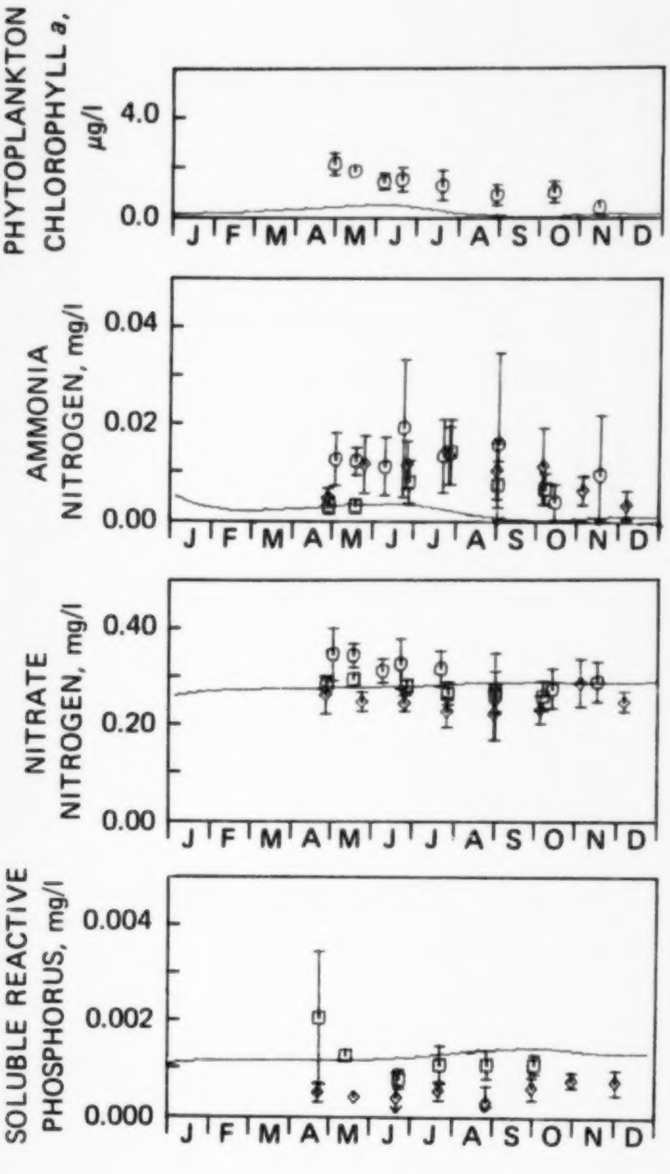


Figure 51. Computed versus Observed Data (So. Lake Huron hypolimnion)

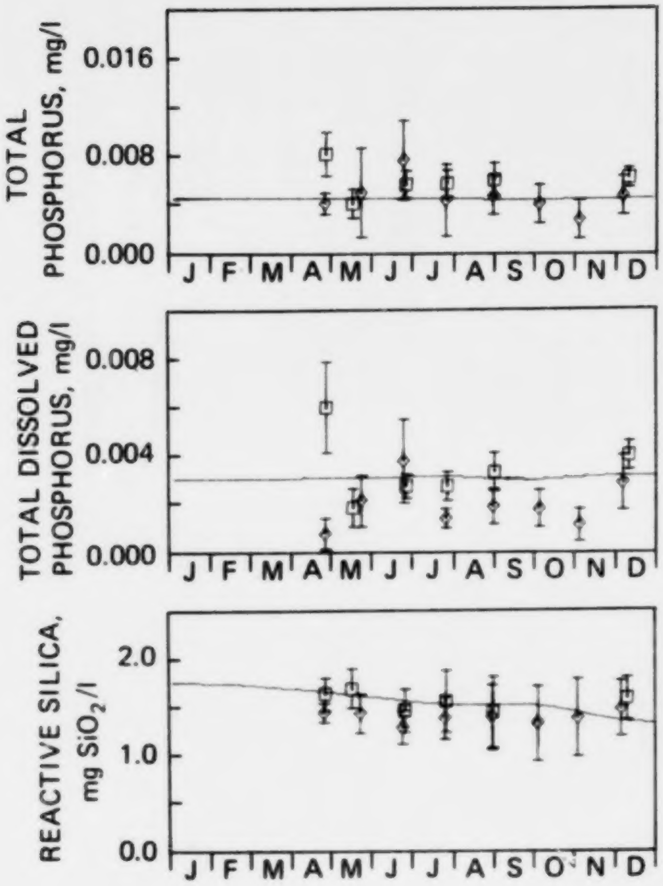


Figure 52. Computed versus Observed Data. (So. Lake Huron hypolimnion)

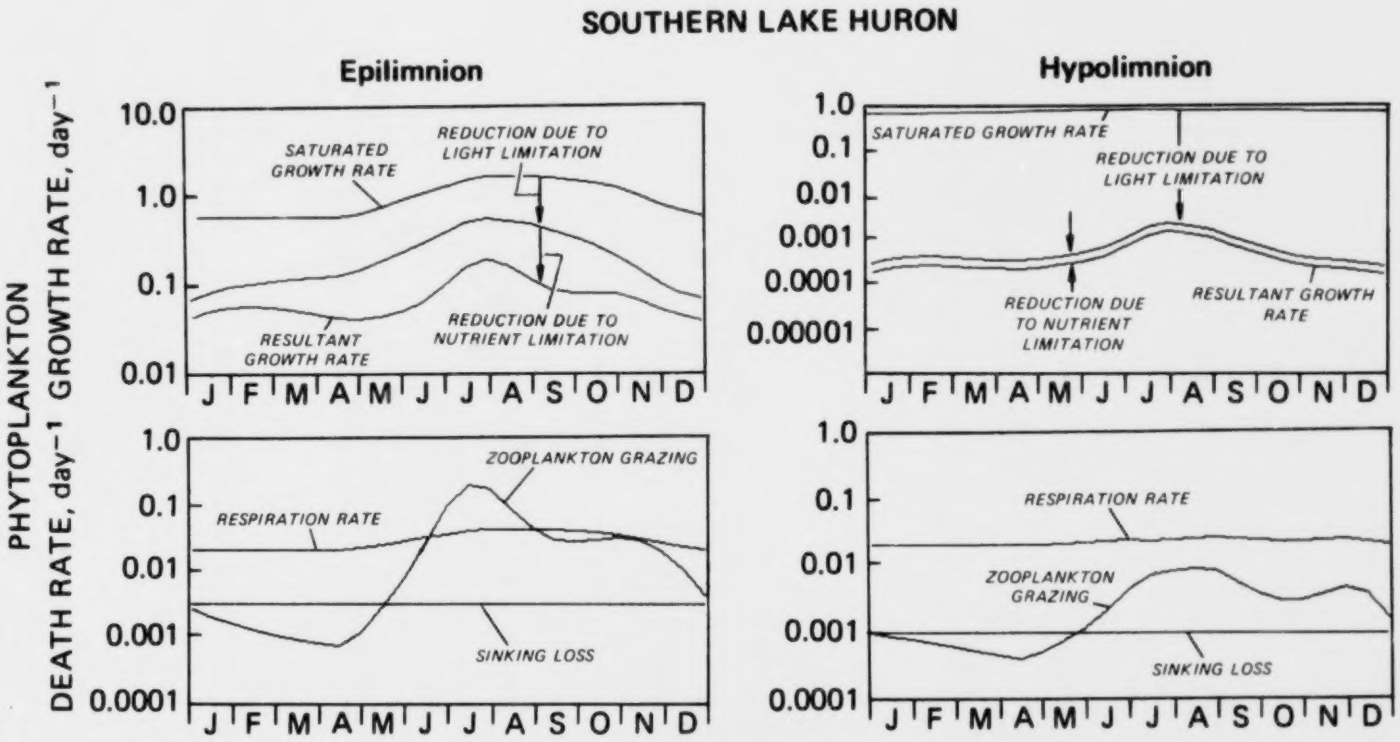


Figure 53. Phytoplankton growth and death rates in Southern Lake Huron epilimnion and hypolimnion.

the effect in some manner such as the inclusion of a light adaptive mechanism. The present kinetics do not deal with this phenomena.

Analysis of the Computation

Figures 54 to 58 present a detailed analysis of the calculation described above. The analysis is presented as a comparison between the open lake waters, as characterized by southern Lake Huron, and Saginaw Bay. This yields further insight into the behavior of the model and the system under study.

The effects of nutrient limitation of phytoplankton growth is shown on fig. 54. Nitrogen is not an important factor in limiting growth in southern Lake Huron, since total inorganic nitrogen concentrations average more than 0.25 mg/ℓ and provide an abundant source for plankton growth. On the other hand, phosphorus limitation is significant yielding up to a 60 percent reduction in the saturated growth rate. This is expected since available phosphorus concentrations in southern Lake Huron are very close to the Michaelis half saturation constant of 0.5 μg P/ℓ.

Saginaw Bay is not nitrogen limited during spring growth but there is a limitation effect during fall growth with reductions up to 30 percent in the growth rate resulting. Phosphorus limitation dominates, however, especially during spring growth where 60 percent reductions result. The replenishment of the available phosphorus pool can be seen as a sharp increase in the limitation term from the beginning of June to mid-July coinciding with the decline in the phytoplankton standing crop and the recycling of unavailable phosphorus.

The sources of unavailable phosphorus available for conversion to forms utilized for growth of phytoplankton is shown in fig. 55. In southern Lake Huron the principal source is from respiring phytoplankton. Phytoplankton grazed but not assimilated by the herbivorous zooplankton contribute significantly to the unavailable phosphorus pool in mid-July when the herbivore population is at a maximum. This is true in Saginaw Bay also where excreted phytoplankton phosphorus contributes significantly to phosphorus available for recycle at the peak of herbivorous phytoplankton growth. Zooplankton respiration and excreted zooplankton phosphorus also provide unavailable phosphorus and their relative importance can be seen.

The unavailable phosphorus flux is higher in Saginaw Bay by nearly an order of magnitude. This is due to the higher concentrations of phytoplankton phosphorus which provides the main kinetic source. The rates are also slightly higher in Saginaw Bay due to the warmer temperatures, but the principal effect is the larger standing stock.

The phosphorus concentrations which develop as a result of phytoplankton uptake and the recycle mechanisms are shown in fig. 56. The figure presents the available phosphorus, then the available plus unavailable phosphorus, and finally the total phosphorus which includes the algal phosphorus as well. Note the larger proportion of unavailable phosphorus in southern Lake Huron when compared to Saginaw Bay. This is primarily the result of

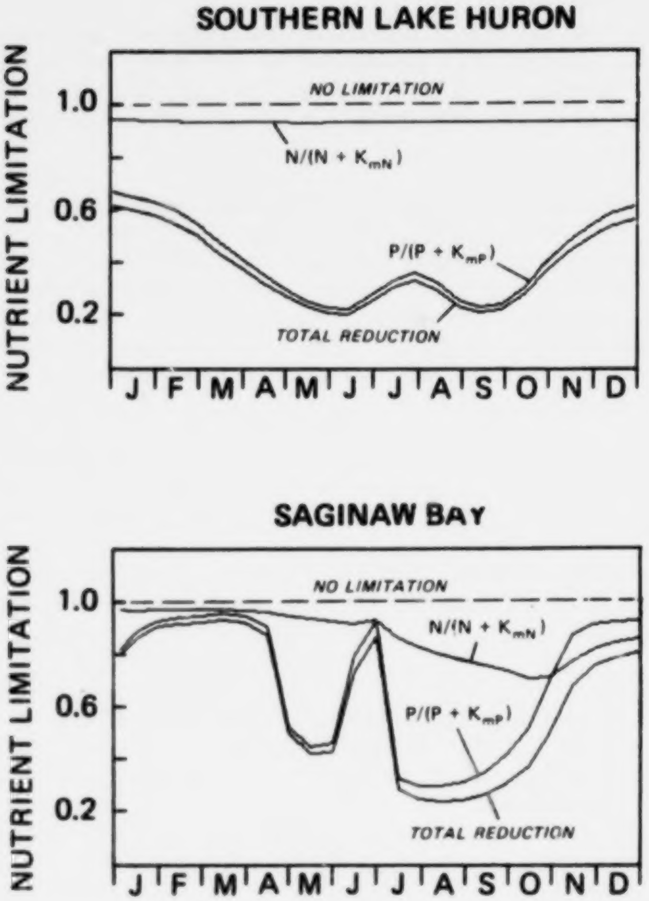


Figure 54. Nutrient limitation of growth rate. Inorganic nitrogen (N/N + KmN) and reactive phosphorus (P/p + Kmp) terms, and their product (total reduction)

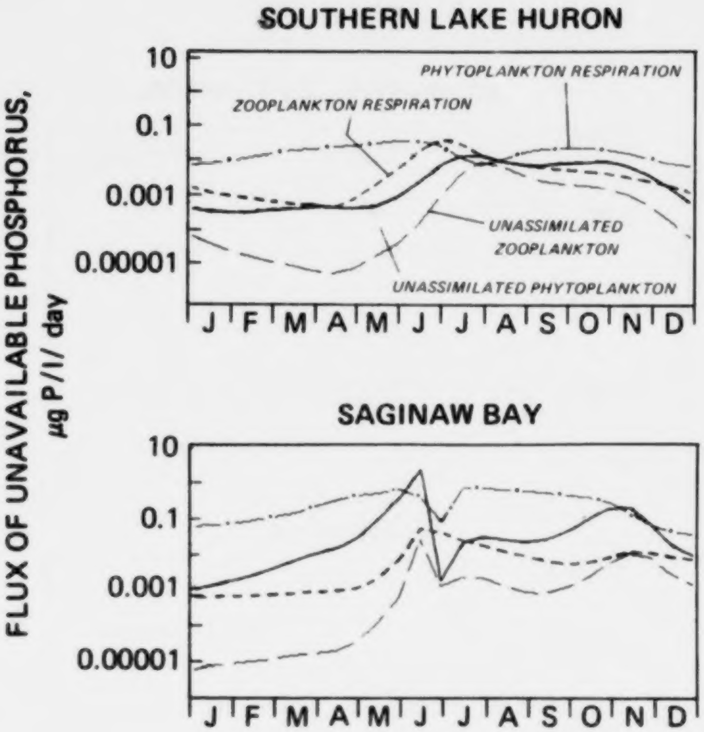


Figure 55. Comparison of kinetic fluxes of unavailable phosphorus in Southern Lake Huron and Saginaw Bay. Curves correspond to $a_{pP}(1-f_A)R_z$ for phytoplankton respiration; $a_{pC}(1-f_A)(R_{5H}+R_{5C})$ for zooplankton respiration; $a_{pP}(1-\beta)(1-f_A)R_3$ for unassimilated phytoplankton, and $a_{pC}(1-\varepsilon_c)(1-f_A)R_4$ for unassimilated zooplankton.

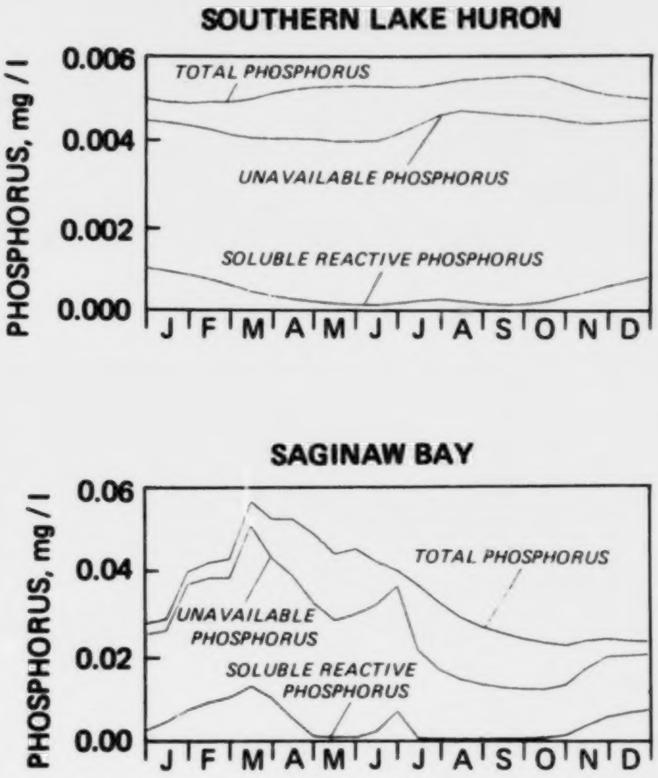


Figure 56. Cumulative plot of the components of total phosphorus in Southern Lake Huron and Saginaw Bay. The curves correspond to reactive phosphorus; reactive & unavailable phosphorus; and total phosphorus, which includes algal and zooplankton phosphorus.

the variable recycle rate which is small in southern Lake Huron and large in Saginaw Bay.

An analysis of the phytoplankton growth and death rates is presented in fig. 57. It can be seen that light limitation is more of a factor in Saginaw Bay than it is in southern Lake Huron. This is expected since the Secchi depth averages 6 meters in the open lake but only 1 meter in Saginaw Bay. Nutrient limitation in Saginaw Bay can be seen to be minimal at the end of June when recycle has replenished the available nutrient pool. Respiration dominates the phytoplankton death term for most of the year in both areas until the herbivorous zooplankton build a significant population and grazing becomes the major factor. These terms peak in both areas at the time of maximum herbivorous zooplankton. In Saginaw Bay, it can be seen from the rapid rate of increase in zooplankton grazing as a major factor in phytoplankton decline, that if no limitation were placed on zooplankton grazing rate as discussed earlier, they would develop large populations which is inconsistent with observations and also exert too much grazing pressure. Instead of the herbivorous zooplankton growth rates leveling off in Saginaw Bay, as shown in fig. 58 the rate would continue to increase. Zooplankton respiration rates are about equal in Saginaw Bay and southern Lake Huron with the slight difference due to warmer Saginaw Bay waters affecting the temperature dependence. Carnivore grazing is seen to be much more significant in Saginaw Bay where more of a standing crop of herbivores are maintained which stimulates carnivore growth and causes the grazing pressure.

The calculations presented above compare reasonably well with observed data for the variables of concern in the different areas of Lake Huron. An analysis of the results has also been presented highlighting some of the important mechanisms such as nutrient limitation, nutrient recycle, and phytoplankton and zooplankton growth and death rates. These processes strongly affect the seasonal distribution of the phytoplankton and nutrients and the calibration is sufficiently sensitive to the values of the kinetic constants so that it is possible to make reasonable estimates of their magnitudes.

There is an important process, however, for which the calibration of the seasonal model is insensitive because its time scale is longer than seasonal. It is the loss of particulate phosphorus to the sediments. The issue of whether Lake Huron is in equilibrium with its current mass inputs of phosphorus depends on the magnitude of the flux of phosphorus to the sediments.

Phosphorus Sedimentation and Lake-wide Mass Balance

The loss of total phosphorus from Lake Huron is primarily the result of sinking of particulate phosphorus into the sediments. The principle forms of phosphorus considered in this calculation are algal-bound phosphorus, unavailable phosphorus and soluble reactive phosphorus, with zooplankton-bound phosphorus a small fraction of the total. Algal phosphorus and the particulate portion of the unavailable phosphorus each have a sinking velocity which eventually leads to a fraction of this material being incorporated into the sediment. This mechanism is represented in the calculation by a sinking velocity across the epilimnion-hypolimnion interface and the same velocity

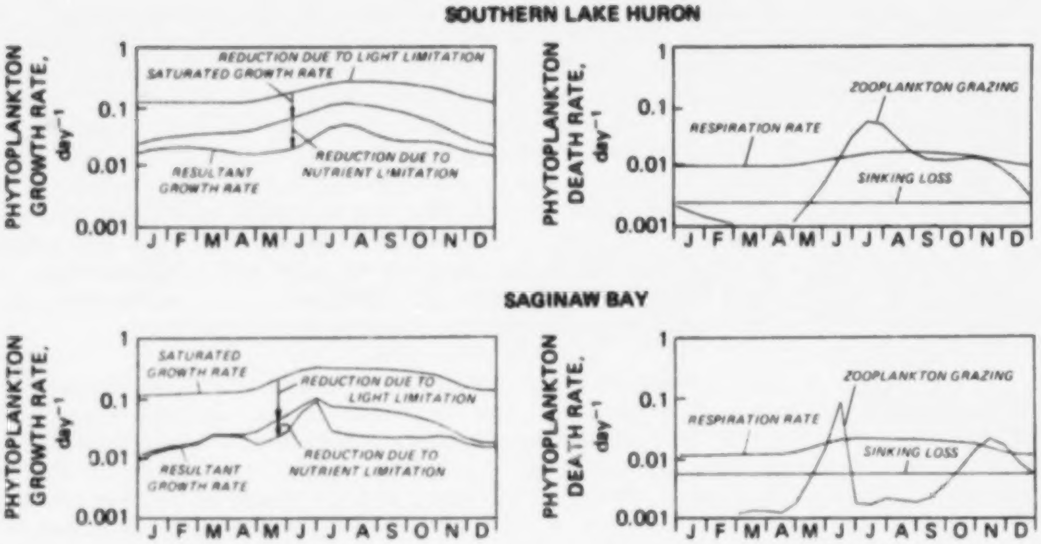
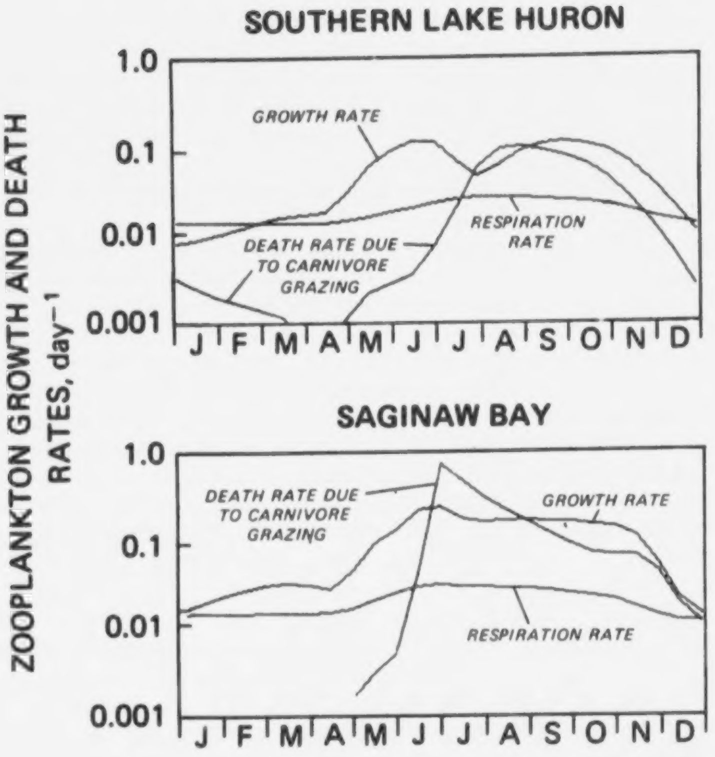


Figure 57. Seasonal distribution of phytoplankton growth and death rates showing light and nutrient limitation reductions.



SOUTHERN LAKE HURON

SAGINAW BAY

Figure 58. Seasonal distribution of computed herbivorous zooplankton growth and death rates for Southern Lake Huron and Saginaw Bay growth rate, $\beta a_{cP}R_3$; respiration rate, $- R_4$; carnivore grazing, $-R_{5H}$.

across the sediment-water interface. For the coarse vertical segmentation used, i.e. two layers, the seasonal calculation of phytoplankton is not very sensitive to the absolute magnitude of the algal settling velocity as shown subsequently in section 9 so that it is not possible to infer this velocity from the calibration. Rather it is necessary to know the flux of phosphorus from independent estimates. The settling velocities are then suitably adjusted to reflect these estimates.

Robbins [97] has estimated the net phosphorus settling into the mud layer of fine grained sediments for Saginaw Bay to be 360 tonnes P/year. For southern Lake Huron, a loss to the sediments is estimated at 782 tonnes P/year. Utilizing loss rates corresponding to an algal settling velocity of 0.05 m/day and a settling velocity of unavailable phosphorus of 0.1 m/day in open lake waters, the model computes a yearly loss of 363 tonnes P/year for Saginaw Bay and 848 tonnes P/year for Southern Lake Huron.

A comparison is also possible to an estimate of the lakewide sedimentation loss based on the Upper Lakes Reference Study mass balance [98] for total phosphorus. Their reported difference between inputs and outputs for the whole lake is 4440 tonnes/yr and for the main lake is 2640 tonnes/yr. Thus, there is a loss in Georgian Bay and the North Channel, areas not included in this model, of 1800 tonnes/yr. Adding this to the model's computed total sedimentation loss of 2626 tonnes/yr yields 4426 tonnes/yr. The lakewide estimate of sediment loading including anthropogenic and natural sources is 4750 tonnes/yr [98]. It is important to realize that these computed sedimentation fluxes are made using the same loss rates in both Saginaw Bay and Lake Huron. The difference is due to different concentrations of settleable phosphorus.

Table 13 summarizes these results and includes a comparison to the IJC-ULRS mass balance of main Lake Huron. The most recent IJC-ULRS estimates of total phosphorus loading are very close to those used in this calculation. The major loss in the main lake segments is via the settling of unavailable phosphorus whereas in Saginaw Bay the principal mechanism is phytoplankton settling. The model computes total outflow that is lower than that measured, although it agrees with the concentrations in southern Lake Huron whose waters exit via the St. Clair River. This apparent discrepancy may be due to local inputs to the St. Clair River. With the settling velocities used in the calculation, Lake Huron is slightly out of equilibrium with respect to its present loading, amounting to a buildup of 364 tonnes of phosphorus during 1974 or approximately a 10% change. Considering the uncertainties of the estimates it is reasonable to conclude that the lake is essentially in equilibrium.

Application to Lake Ontario

In order to further strengthen the calibration of the Saginaw Bay-Lake Huron model, and to investigate the generality of the proposed recycle kinetic structure an application to Lake Ontario is presented. In terms of nutrient and chlorophyll concentrations, Lake Ontario is intermediate between Saginaw Bay and Lake Huron. It, therefore, is an ideal test case for the modified recycle kinetics, and in fact served as a guide for the ultimate choice of the half-saturation constant for recycle.

TABLE 13. TOTAL PHOSPHORUS MASS BALANCE

	Total Phosphorus Load	Loss From Phytoplankton Sinking	Loss from Sinking of Unavail. P	Total Loss to Sediment	Estimate from Sediment P Profile [97]
		(metric tons/year)			
No. Lake Huron	1,281	66	1,349	1,415	
So. Lake Huron	1,297	30	818	848	782
Saginaw Bay	1,315	294	69	363	360
	3,893	390	2,236	2,626	

	Model	IJC-ULRS [105]
Total Input	3,893	3,720
Sedimentation Loss	2,626	2,640 (loss + buildup)
Output St. Clair River	900	1,080
Phosphorus Buildup	364	

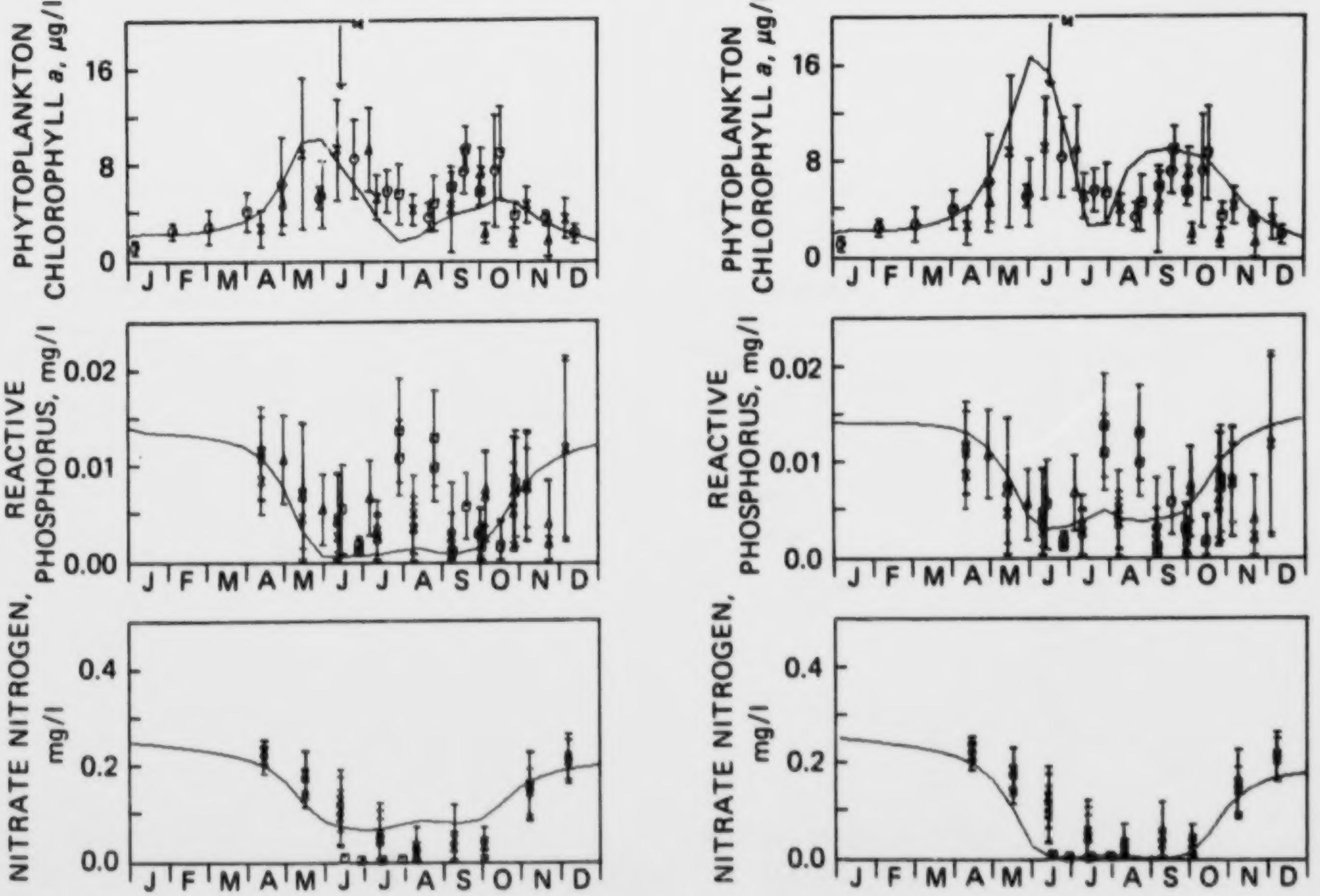
Two major modifications have been made to the recycle kinetics when compared to those used initially in Lake Ontario [48]. The recycle rates for nitrogen and phosphorus are assumed to be the same, and the rate changes with changing chlorophyll concentration as described previously. Also a fraction of the nutrient fluxes due to respiration and excretion are assumed to be immediately available. The result of these kinetics when applied to Lake Ontario with all other parameters the same as in the previous calibration [48] is shown in fig. 59a. As can be seen the predicted fall peak is low when compared to observed values from 1967 thru 1972 CCIW cruises of Lake Ontario. Computed reactive phosphorus concentrations are within the range of observed data but computed nitrate nitrogen values are larger than observed towards the end of the year. This is due to the low fall phytoplankton population that is calculated and consequently too little nitrate utilization.

The second calculation, figure 59b, illustrates the result of not only incorporating the changes outlined above but also the phosphorus to chlorophyll ratio of the Lake Huron/Saginaw Bay model of 0.5 μg P/μg Chℓ-a. Both the calculated spring and fall phytoplankton peaks are too large. Reactive phosphorus utilization is not as great as in the previous example and it can be seen that the low calculated nitrate concentrations indicate that nitrogen has become limiting.

The results of this exercise indicate that the carry-over of the kinetic changes affecting the nutrient cycles from the Lake Huron/Saginaw Bay model to the Lake Ontario model do not have drastic effects on the computation, although the chlorophyll verification is not as good as the original model. Figure 60 shows a final calibration for Lake Ontario with the Lake Huron nutrient kinetics. It utilizes a phosphorus to chlorophyll ratio of 0.5 μg P/μ Chℓ-a and a slightly lower initial condition for reactive phosphorus (10 μgPO_4- P/ℓ versus 14 μgPO_4- P/ℓ) used previously. The results are quite reasonable although the spring peak is slightly larger than observed. It is reassuring that reactive phosphorus compares fairly well in the hypolimnion as well. This is due to the proportional recycle effect. Phytoplankton concentrations are not as high in the hypolimnion as in the epilimnion and therefore the recycle rate is lower. This low rate prevents a buildup in the lower layer. Figure 61 presents the final chlorophyll-a calculations for southern Lake Huron, Lake Ontario, and Saginaw Bay.

These calculations embody the same phytoplankton growth and respiration kinetics, and the same recycle kinetics. The range over which these kinetics apply is approximately an order of magnitude in chlorophyll-a concentration and almost two orders of magnitude in primary production. It is remarkable that not only the same equation structure applies but also that the same kinetic constants are applicable. This observation suggests that the kinetic constants and functional relationships have a fundamental basis.

A set of constants that result from a single calibration of a single, rather homogeneous, setting are usually not regarded as certain until some verifications are performed using independent data. The kinetics employed in the calculation displayed in fig. 61 have not been verified in this sense. However they have been shown to have general applicability to three separate regions with widely varying characteristics. This display of con-



Phosphorus-chlorophyll ratio = 0.001 mg P/µg Chl *a*

Phosphorus-chlorophyll ratio = 0.0005 mg P/µg Chl *a*

Figure 59. Lake Ontario calibration. Application of saturating recycle kinetics. Data for 1967 - 1972 CCIW cruises.

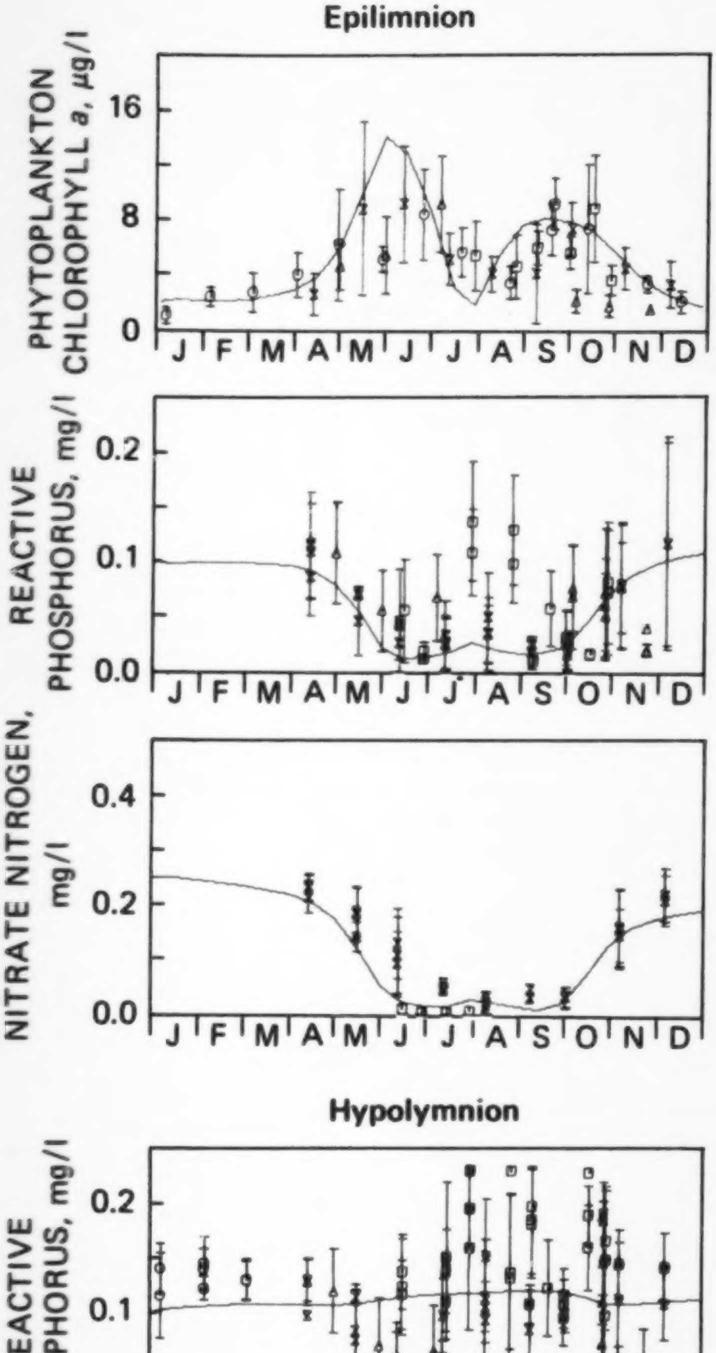
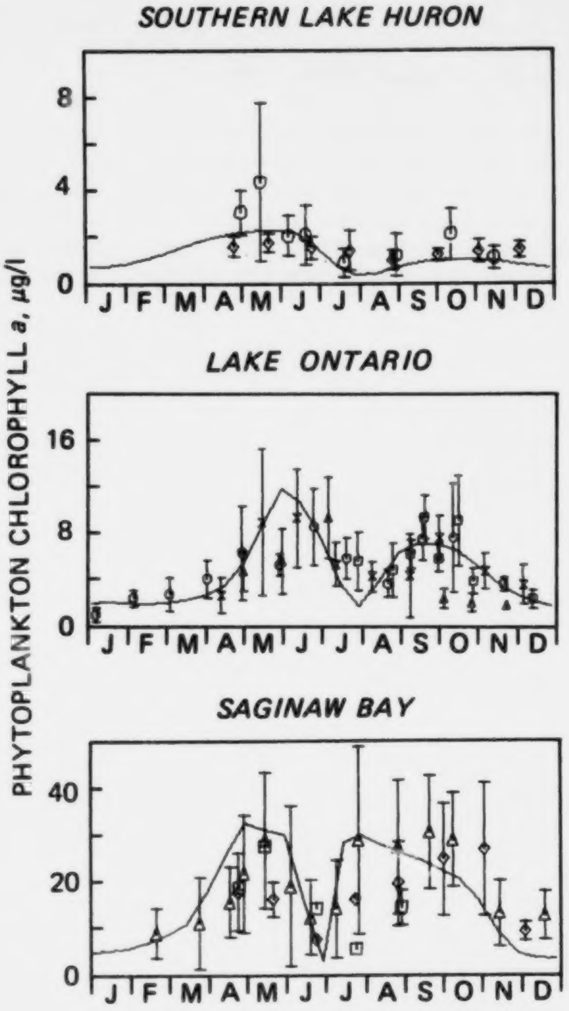


Figure 60. Lake Ontario Calibration



61. Final calibration computations for Southern Lake Huron, Lake Ontario, and Saginaw Bay phytoplankton chlorophyll. The phytoplankton and recycle kinetic constants are the same in each calculation. However Lake Ontario zooplankton kinetics are not those used for Lake Huron and Saginaw Bay.

sistency argues rather strongly that the results are more than just a calibrated calculation (or as it is sometimes put, a curve fit) but rather that they have a certain generality. This is somewhat surprising and gratifying if one considers that the processes have been idealized greatly in an attempt to make their quantitative description tractable.

By the same token the zooplankton kinetic constants used are different for Lake Ontario than the Lake Huron/Saginaw Bay calculation and it is reasonable to conclude that this generality cannot be claimed for these kinetics. As shown in the next section, the zooplankton responses are very sensitive to the magnitude of the coefficients employed which also suggests that the structure is not as robust as the phytoplankton kinetics.

SECTION 9

SENSITIVITY ANALYSIS

One of the means available for testing the quantitative framework employed in this study is to perform a series of calculations in which the sensitivity of a model to its coefficients is determined. These coefficients are chosen within the range of reported values, and are the result of many calibration runs. However there is frequently a range of values which may be assigned and it is important to know what effect, if any, adjusting these coefficients has on the resulting computations.

The coefficients chosen for investigation are those which affect primary variables and are related to important aspects of the calibration procedure. Since phytoplankton chlorophyll is a key variable, several coefficients directly related to its kinetics are investigated:

1) phytoplankton growth rate: K_1
2) phytoplankton respiration rate: K_2
3) temperature dependence of phytoplankton growth rate: θ_1
4) zooplankton grazing rate: K_3
5) phytoplankton settling velocity: w_p
6) saturating light intensity for phytoplankton growth: I_S

Coefficients affecting the inorganic nutrient systems, particularly phosphorus, are also investigated:

1) Half saturation constant for available phosphorus: K_{mp}
2) Phosphorus to chlorophyll ratio: a_{pP}
3) Rate of recycle of unavailable phosphorus and nitrogen to available forms: K_7 and K_8

Other effects investigated are:

1) vertical transport (stratification) effects
2) silica to chlorophyll ratio: a_{SiP}

The results of these sensitivity runs are presented as a series of plots showing the effect of parameter changes compared to the calibrated model results previously presented. Normally, sensitivity effects are investigated by ± 50 percent changes in the value used for model calibration, thus bracketing the results.

Figure 62 shows the effect of varying the phytoplankton growth rate term, K_1. Using a value of 2.08 day^{-1} reproduces the bimodal phytoplankton growth curve in Southern Lake Huron and Saginaw Bay fairly well. When the rate is increased to 3.12 day^{-1}, initial growth occurs earlier with the higher growth rate compensating for temperature limitation during these colder months causing a broader spring pulse in both areas. Lowering the rate to 1.04 day^{-1} has dramatic effects on both areas. In Southern Lake Huron, the spring peak occurs late and the magnitude of both this and the fall peak is lower. The spring pulse in Saginaw Bay is much lower with the lower rate being unable to overcome the combination of temperature, light, nutrient limitation effects and transport losses.

The effects of varying the phytoplankton endogenous respiration rate, K_2, is also shown in fig. 62. Lowering the rate from .05 to .025 day^{-1} increases the concentration of phytoplankton chlorophyll both in Southern Lake Huron and Saginaw Bay as one might expect since a sink of phytoplankton is reduced. Increasing the rate causes more loss due to endogenous respiration to occur and lower phytoplankton concentrations result. It is interesting to note that the timings of the pulses and declines are virtually unaffected.

Figure 62c illustrates the effect of varying the temperature dependence of phytoplankton growth. Since the effects of the saturated growth rate, K_1, and the temperature dependence, θ_1, are compounded in the growth rate term, and in order to isolate the effect of temperature dependence the saturated growth rates term for the three examples are set to be the same at 13°C. This corresponds to the approximate temperature during spring bloom.

As can be seen, lowering θ_1 from 1.068 (K_1 = 2.08 day^{-1}) to 1.034 (K_1 = 1.65 day^{-1}) increases the growth rate during colder periods and spring growth starts earlier in both Southern Lake Huron and Saginaw Bay. Increasing θ_1 to 1.102 (K_1 = 2.59 day^{-1}) results in the opposite effect, a delayed spring pulse which is less broad. The timing and magnitude during the fall period are virtually unaffected in both areas of the lake.

Since phosphorus limitation has been shown to be an important mechanism during the calibration process, the next series of sensitivity runs addresses parameters affecting this process. Figure 63a shows the effect of varying K_{mp}, the half saturation constant for inorganic phosphorus, and a_{pP}, the phosphorus to chlorophyll ratio. Increasing the half saturation constant from 0.5 μg P/ℓ to 1.0 and 2.0 μg P/ℓ has virtually no effect on Saginaw Bay, where concentrations of soluble reactive phosphorus average approximately 5 μg/ℓ, well above the half saturation value. There is a sufficient inorganic phosphorus supply available for spring growth to commence as soon as temperature and light conditions warrant it. In Southern Lake Huron, however, soluble reactive phosphorus concentrations average near 0.5 μg P/ℓ which is right at the K_{mp} value of the calibrated model. Any increase in this value results in a higher degree of nutrient limitation. At 1.0 μg P/ℓ spring growth starts later since higher temperature and better light conditions are needed to overcome the added nutrient limitation. At 2.0 μg P/ℓ this effect is even more pronounced. Soluble reactive phosphorus concentra-

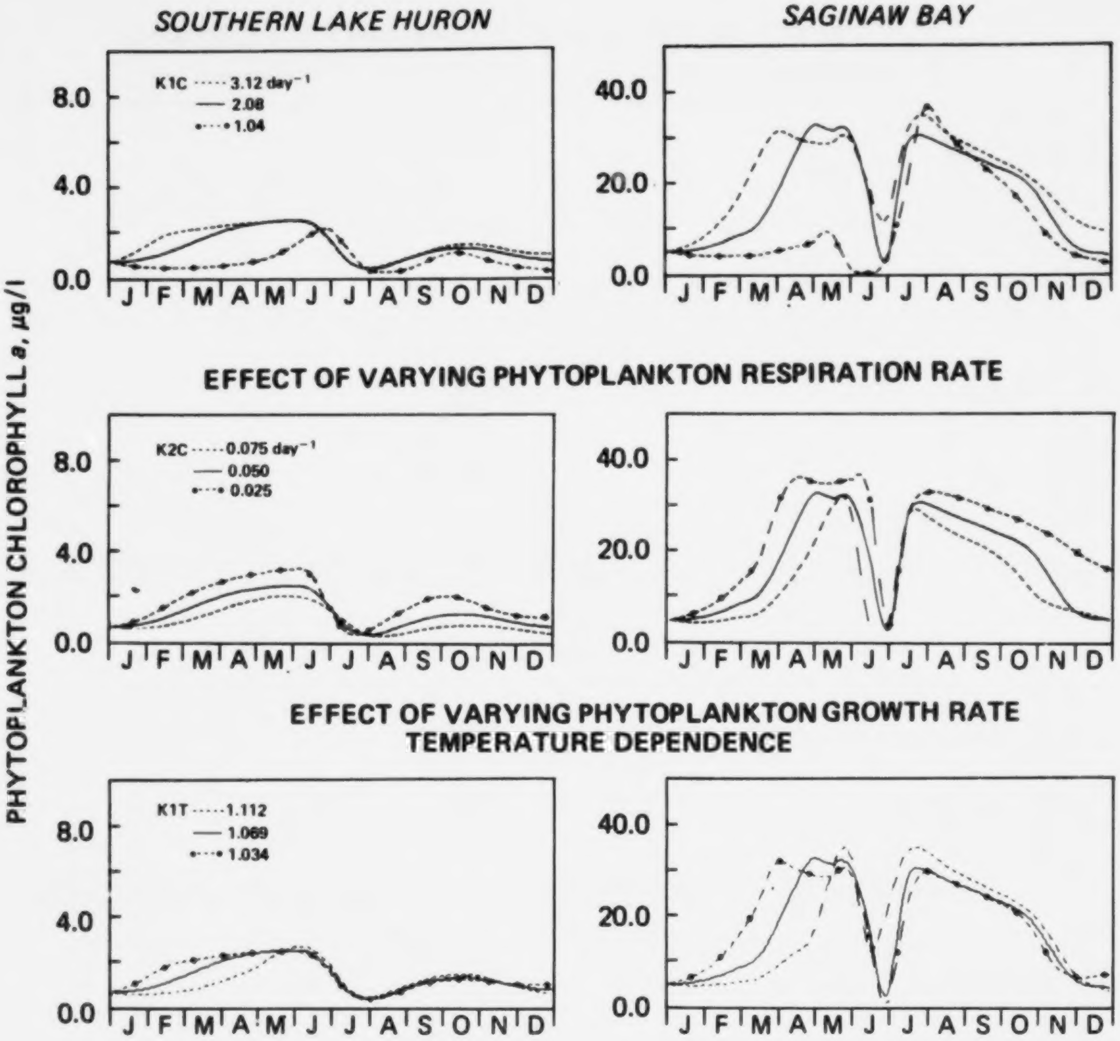


Figure 62. Sensitivity to phytoplankton kinetic constants. Saturated growth rate @ 20°C, K_1 (top). Respiration rate @ 20°C, K_2 (middle). Growth rate temperature dependence, θ, with $K_1\theta_1^{T-20}$ constant at T = 13°C (bottom). Labels in the figures correspond to computer program variable designations.

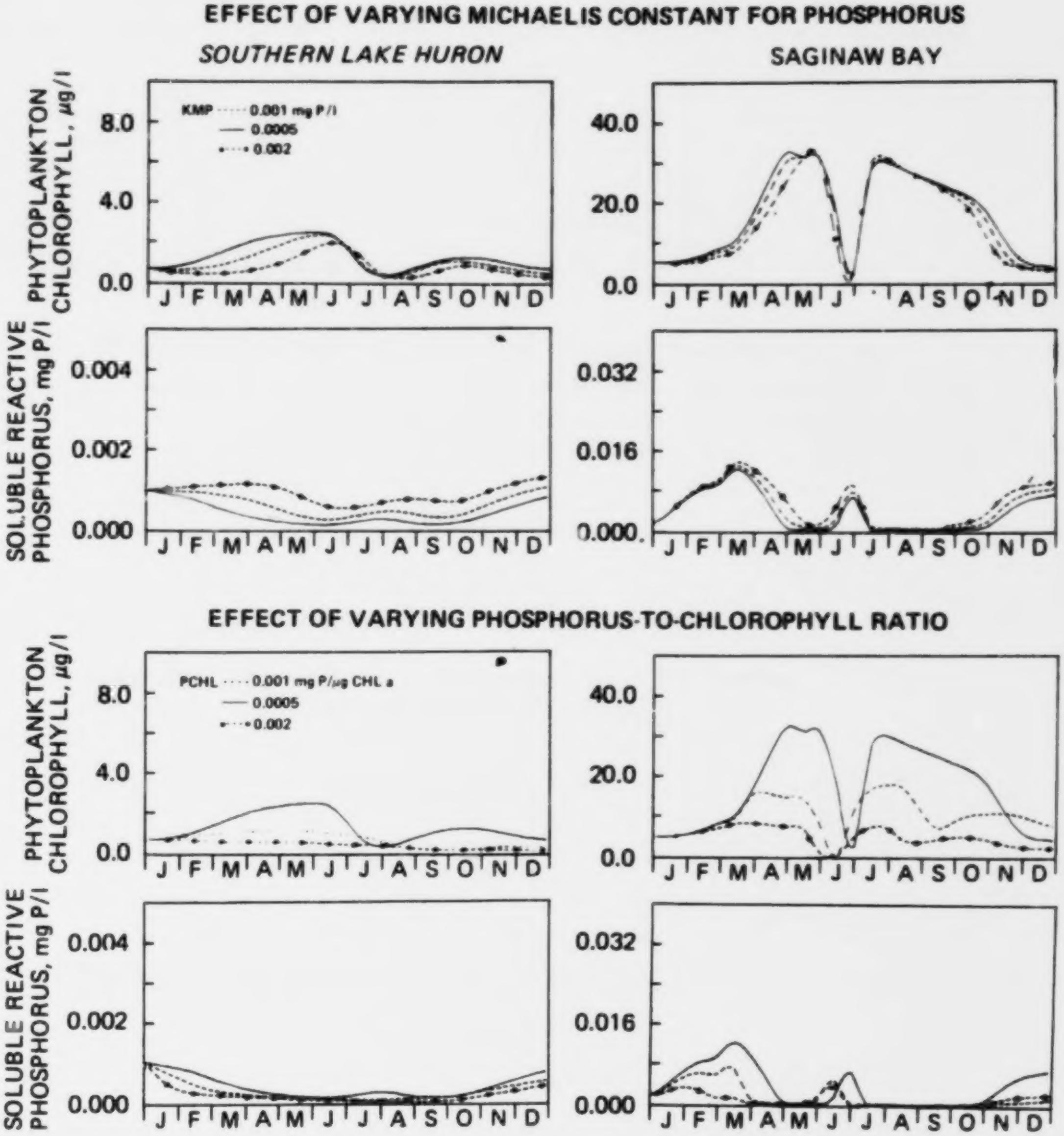


Figure 63. Sensitivity to phosphorus system kinetic constants. Michaelis constant for phosphorus, K_{mp} (top). Phosphorus to chlorophyll ratio, a_{pP} (bottom).

tions follow the inverse pattern. Since limited growth implies less nutrient uptake, it follows that higher concentrations of inorganic phosphorus are computed with increasing values of K_{mp}.

The effects of varying the phosphorus to chlorophyll ratio, a_{pP} = PCHL, are investigated in fig. 63b. This coefficient effectively governs how much available phosphorus is utilized to produce a unit of chlorophyll a. As a_{pP} is increased the available supply of inorganic phosphorus will be depleted more rapidly. The calibrated model uses a value of 0.5 μg P/μg Chℓ-a. It can be seen that doubling and redoubling this value to 1.0 and 2.0 μg P/μg Chℓ-a has drastic effects on the calculation since two and four times the amount of phosphorus is being utilized by the phytoplankton for growth. In Southern Lake Huron a spring pulse of the magnitude observed is never generated and the fall peak suffers as well. Soluble reactive phosphorus concentrations are depleted to below the half saturation value and growth becomes severely limited. In Saginaw Bay the effect is equally dramatic. The spring peak is only about 15 μg/ℓ chlorophyll a using a_{pP} = 1.0 μg Chℓ-a/μg PO_4-P and less than 10.0 μg/ℓ at a value of 2.0. These concentrations are well below observations. The increased rate of depletion of the soluble reactive phosphorus pool is also clearly seen. At a_{pP} = 2.0 μg P/μg Chℓ-a the available pool is essentially depleted by the end of March and phytoplankton growth levels off. Some initial buildup of reactive phosphorus due to pulses of phosphorus from the Saginaw River (Section 4) occurs at a_{pP} = 1.0 μg P/μg Chℓ-a but not enough to sustain a spring phytoplankton pulse of the magnitude observed. Thus, although a phosphorus to chlorophyll a rate of 0.5 μg P/μg Chℓ-a is at the low end of the range of reported values, the concentrations of inorganic phosphorus in the open lake waters are small. Further the standing crop of phytoplankton which must be supported in Saginaw Bay is large. The computation is able to simultaneously reproduce observed conditions in both areas only for a value of a_{pP} at this level.

The importance of a correct phosphorus to chlorophyll a stoichiometric coefficient is clear from these sensitivity calculations. It is also suggested by eq. (56) of section 6 which indicates that the quantity of the total phosphorus that appears as chlorophyll is inversely proportional to the stoichiometric coefficient. The Lake Ontario results, see fig. 59 and 60, also support this inverse relationship. One of the principal drawbacks of Monod kinetics is that this ratio is assumed to be fixed. However it is well known that this ratio is quite variable and depends on the ambient phosphorus concentration. Thus it appears that an important refinement would be a kinetic structure which reflects this variability. Bierman's Saginaw Bay calculation [99] is one such structure, and a detailed analysis of this phenomena is available [37]. The choice of a minimum ratio is consistent with the discussion in section 6 and the observed data.

The coefficient governing the rate of recycle of nutrients from the unavailable to an available inorganic form is assumed to apply to both the unavailable phosphorus and nitrogen. Figure 64 shows the results of sensitivity calculation with doubled and halved coefficients, $K_7 = K_8$, the

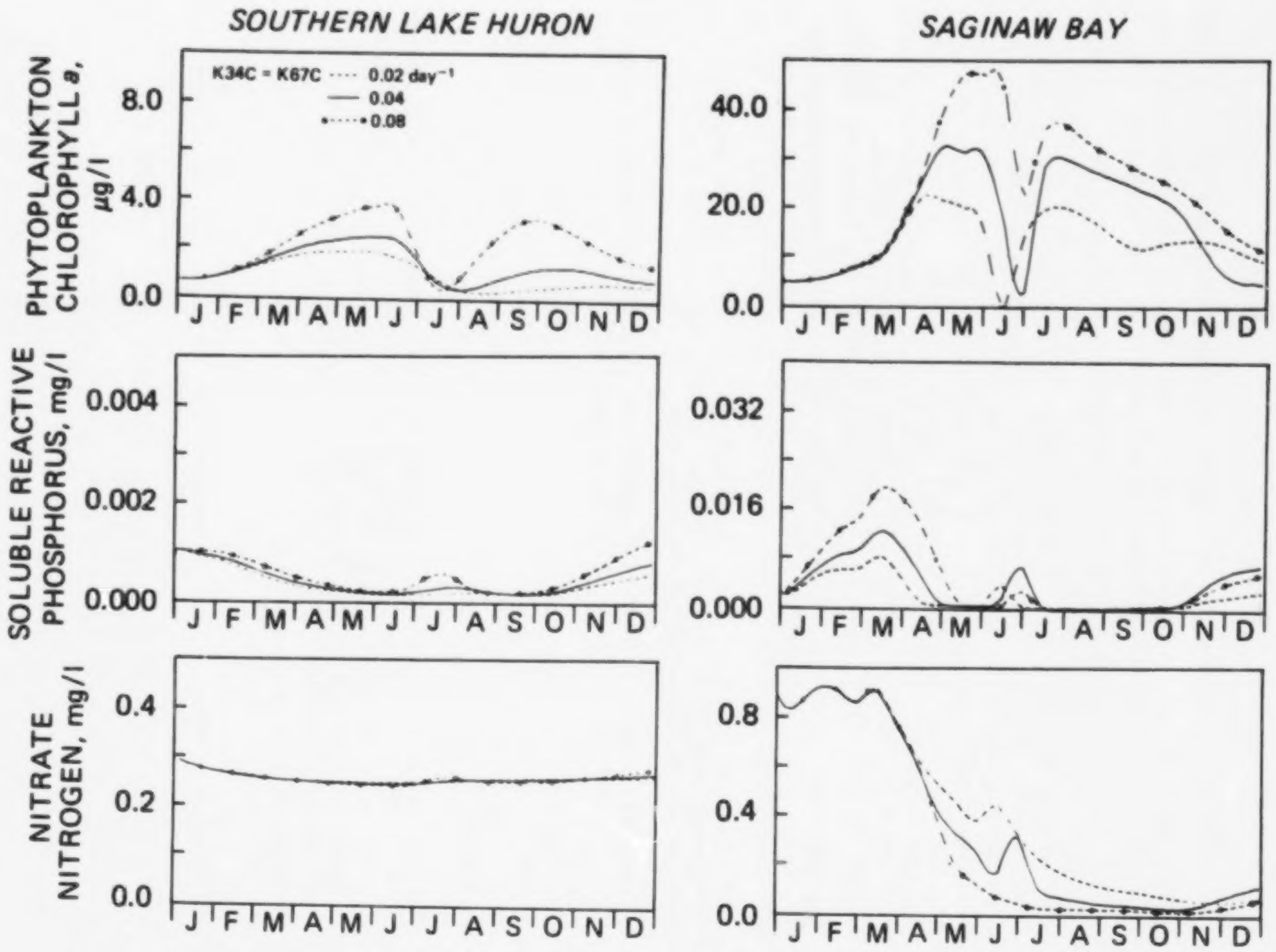


Figure 64. Sensitivity to recycle rate kinetic constant of phosphorus and nitrogen, phytoplankton chlorophyll, reactive phosphorus, and nitrate nitrogen.

recycle rates of organic nitrogen and unavailable phosphorus, respectively. Increases in the recycle rate result in higher calculated phytoplankton chlorophyll and soluble reactive phosphorus concentrations as expected from the theoretical analysis in section 6. As the calibrated rate 0.04 day^{-1} is increased to 0.08 day^{-1} more nutrient replenishment and utilization occurs with larger populations resulting. As a lower rate (0.02 day^{-1}) the converse is true and lower concentrations result. The nitrate profile in Southern Lake Huron is virtually unaffected by changes in the rate of recycle since the recycled nitrate is a small fraction of that already present, while in Saginaw Bay differences occur during the time of reduction in the spring phytoplankton pulse. These reflect a combination of the change in recycle flux and nitrification effects. The ammonia profile in both areas reflects the respective change in concentration due to increases or decreases in the recycle rates.

The effects of changes in herbivorous zooplankton grazing rates is shown on figure 65a. It can be seen that timing of phytoplankton growth and decline is greatly affected by changes in zooplankton grazing. This is true in both Southern Lake Huron and Saginaw Bay. Total zooplankton (herbivores plus carnivores) response also shows marked changes with a lower rate resulting in a delayed pulse in Southern Lake Huron and a delayed and smaller pulse in Saginaw Bay. The higher grazing rate results in earlier growth and more cropping of the spring phytoplankton crop in both areas of the lake.

The model is very sensitive to changes in the herbivorous zooplankton grazing rate as well as the other zooplankton kinetic coefficients. With many factors affecting grazing it is difficult to specify what the actual grazing, efficiency, and limitation coefficients should be. However, the model is able to reproduce observed conditions fairly well. The coefficients governing the zooplankton systems in this model should not, therefore, be thought of as strictly unique. In fact there appears to be considerable uncertainty at the level of the kinetic structure itself. When a calculation is unduly sensitive to coefficients about which little is known, or which are known to vary over orders of magnitude, then considerable caution is required in interpreting the results of the calculation. This appears to be the case with the zooplankton formulation used in these calculations.

However it is important to note that although the shape changes markedly the peak concentrations of phytoplankton chlorophyll are essentially the same over a four-fold change in filtering rate coefficient and the yearly average concentrations are not dramatically different. Therefore although the shape of the seasonal distribution is markedly affected, the characteristic concentrations which are important in projected conditions are not as sensitive to this parameter of the zooplankton kinetics, and it is probable that for peak and average concentrations, the projected conditions are reasonably reliable.

Figure 65b illustrates the effect of varying a_{SiP} the silica to chlorophyll ratio. Although the model is able to match open lake silicate concentrations it fails to reproduce observed concentrations in Saginaw Bay. The reason is that without the inclusion of a diatom group the proper uptake rate

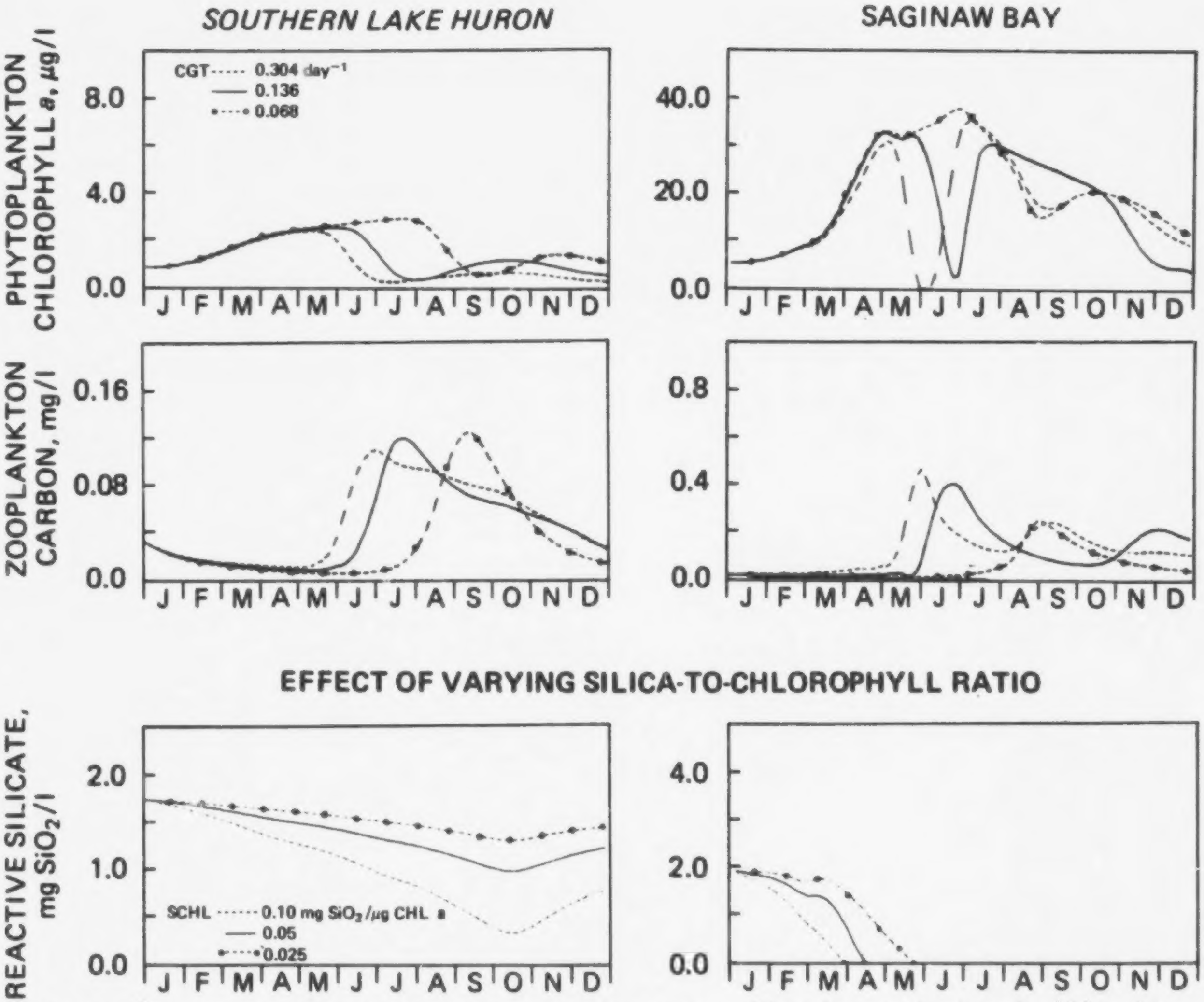


Figure 65. Sensitivity to herbivore grazing rate. Kinetic constant and silica to chlorophyll stoichiometric constant a_{siP}.

is not calculated. Also remineralization of silica is not taken into account. Varying a_{SiP} does not help the situation in the bay, since rapid depletion is calculated even at a lower stoichiometric coefficient. Since the calculation is not structured to represent the silica cycle in Lake Huron/Saginaw Bay, this exercise serves to demonstrate that a diatom species must be added to the calculation if observed conditions are to be reproduced. It also illustrates that an incorrect kinetic structure cannot be tuned arbitratily to fit observations. Thus a calibrated model is an indication that the kinetic structure and constants are not inconsistent with the observations. For silica it is clear that both recycle and selective uptake by diatoms are required for calibration.

The final sensitivity results, fig. 66, illustrate the effects of phytoplankton settling velocity, saturating light intensity, and stratification. As shown earlier, the model is unable to reproduce observed chlorophyll concentrations in the hypolimnion of Southern Lake Huron. Increasing the phytoplankton settling velocity has no effect on the results in the hypolimnion with the increased downward flux of plankton adding little to concentrations in this large volume of water. The increased rate does affect the Saginaw Bay calibration, however, as can be seen. A lower settling rate results in expected higher concentrations.

Increasing the vertical mixing during stratification and allowing more phytoplankton to exchange into the lower layer is another, although unlikely, mechanism by which higher concentrations in the hypolimnion might be calculated. However, there is virtually no effect on the phytoplankton chlorophyll distribution in the lower layer when stratification effects are removed. Thus, changes in transport in the form of phytoplankton settling velocity and vertical exchange as well as a lower saturating light intensity cannot account for high hypolimnetic chlorophyll concentrations. Once the mechanisms for survival at these deep, dark, and colder depths are known perhaps they can be incorporated into the model structure.

The sensitivity calculations outlined above have shown what the effects of changes in kinetic coefficients have on the calculated results. For the phytoplankton and recycle kinetics, even large changes in coefficient values do not produce any computational difficulties and yields results which are plausible. Unfortunately the same is not true of the zooplankton kinetics. The coefficients finally chosen are based on the results of numerous calibration runs, application to Lake Ontario and the constraints provided in the available experimental information. By examining the effects of changes in these coefficients through a sensitivity analysis, one is able to respond to questions of effects of uncertainty in these values.

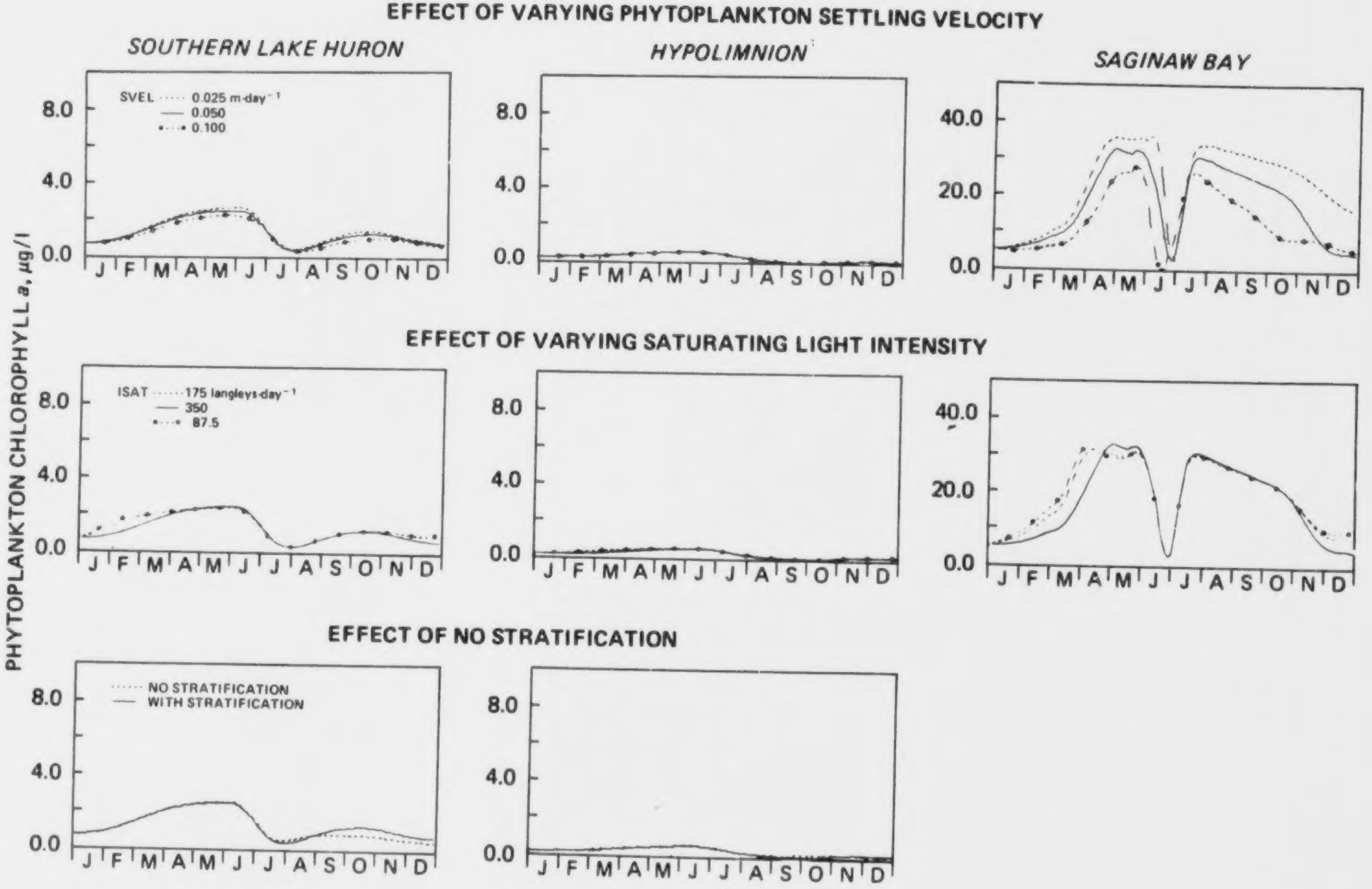


Figure 66. Sensitivity to phytoplankton settling velocity (top), saturating light intensity (middle) and stratifications (bottom), Southern Lake Huron epilimnion (left), Southern Lake Huron hypolimnion (center), Saginaw Bay (right).

SECTION 10

PRELIMINARY APPLICATIONS

The calculation of the response of Lake Huron to increase in phosphorus mass inputs is one of the objectives of this study. In addition to their value for management decisions these calculations also provide considerable insight into the workings of the kinetics.

Simulations are presented for a time span of 15 years. This is considerably shorter than the hydraulic detention time for the whole lake of 22.6 years. However the model does not incorporate the volumes associated with Georgian Bay and the North Channel which reduces the hydraulic detention time of the five segments to 14.1 years. Phosphorus removal via settling considerably lowers the time to steady state. A fifteen year time span appears to be reasonable as shown in fig. 67 which shows the change in yearly average phytoplankton chlorophyll a concentrations in Southern Lake Huron during a fifteen year time span. This projection, based on the final calibrated version of the model presented earlier and the present inputs of nutrients, shows yearly average phytoplankton chlorophyll a concentrations in Southern Lake Huron increasing from 1.33 μg/ℓ at the end of the first year to 1.52 μg/ℓ at the end of the fifteenth year, a 14% increase. The concentration can be seen to level off, approaching dynamic equilibrium with the percent change approaching zero. All projections presented subsequently are fifteen year runs.

Table 14 summarizes the results for a series of such calculations. The values presented cover three phosphorus loading increases for the three different recycle mechanisms, with each simulation lasting fifteen years. There are differences in the base line for each case with respect to phosphorus loading and equilibrium chlorophyll concentrations and direct comparisons of absolute magnitudes are difficult. Therefore the results are converted to percentage changes for ease in comparison of the effects of the differing recycle mechanisms. As shown in fig. 68a, the first order recycle kinetics predict a strictly proportional increase in algal chlorophyll relative to a change in total phosphorus input. However both saturating and second order recycle kinetics predict a more rapid change in algal chlorophyll. This effect is due entirely to the changing quantity of unavailable phosphorus as the recycle rate increases. The total phosphorus concentrations are changing in almost direct proportion to the increasing mass input as shown in fig. 68b. However whereas the change in unavailable phosphorus is proportional for the first order kinetics, fig. 68c, the change is less for saturating kinetics and almost zero for second order kinetics. As a result the proportion of total phosphorus that is algal phosphorus changes dramatically for second order kinetics, almost as dramatically for saturating kinetics, but very little for first order recycle kinetics, fig. 68d.

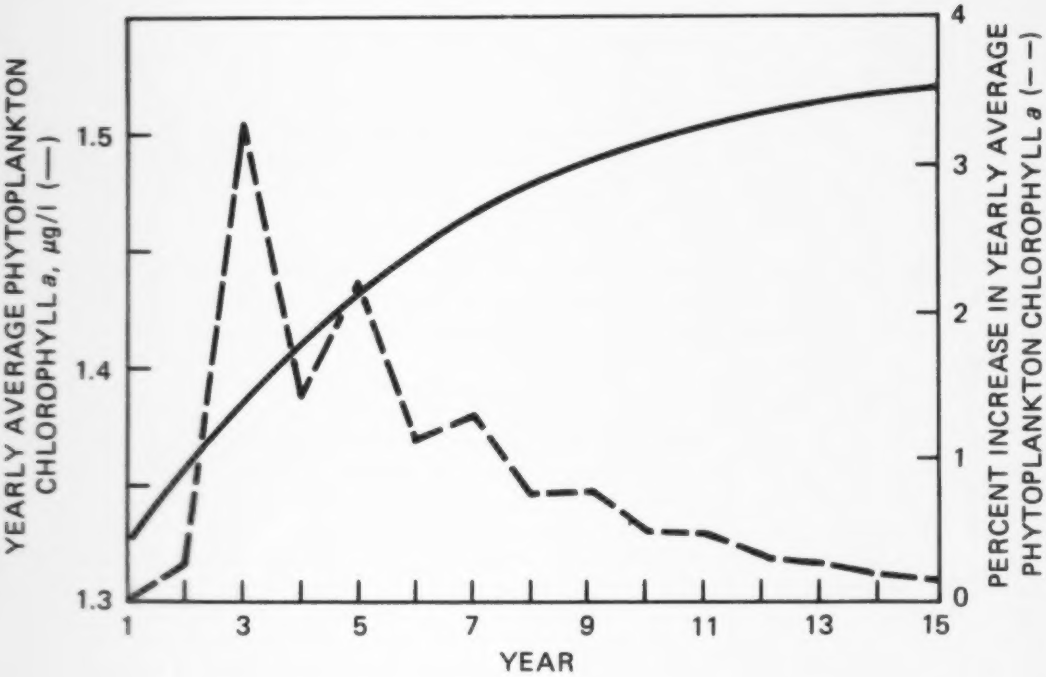


Figure 67. Fifteen year distribution of and percent increase in yearly averaged phytoplankton chlorophyll a in Southern Lake Huron. Model is essentially at steady state in year 15.

TABLE 14. EFFECT OF VARIOUS NUTRIENT RECYCLE MECHANISMS AND INCREASING PHOSPHORUS LOADING: LAKE HURON

		Nutrient Recycle Mechanism		
Percent Change in Total P Load		First Order Recycle Rate	Saturating Recycle Rate	Second Order Recycle Rate
+ 100%	Total P Load(lbs/day)	48,274	44,338	48,274
	Sedimentation Loss(lbs/day)	27,558	28,745	23,210
	Yrly Avg Chlorophyll(μg/ℓ)[#]	5.54	4.94	10.38
	Unavailable P/Total P[#]	0.80	0.87	0.56
+ 50%	Total P Load(lbs/day)	36,205	33,253	36,205
	Sedimentation Loss(lbs/day)	20,749	22,768	19,928
	Yrly Avg Chlorophyll(μg/ℓ)[#]	4.07	2.73	6.27
	Unavailable P/Total[#]	0.79	0.89	0.71
BASE	Total P Load(lbs/day)	24,137	22,169	24,137
	Sedimentation Loss(lbs/day)	13,950	16,134	15,762
	Yrly Avg Chlorophyll(μg/ℓ)[#]	2.66	1.12	2.05
	Unavailable P/Total P[#]	0.78	0.01	0.82

[#] Southern Lake Huron Epilimnion Values

As shown in section 6, the saturating kinetics appear to be the most realistic formulation for the Great Lakes. At chlorophyll concentrations that are large relative to the half saturation constant for the recycle reaction, K_{mr} = 5 μg Chℓ-a/ℓ, saturating kinetics behave as first order kinetics with roughly proportional changes in chlorophyll for changes in total phosphorus loading. However in the range of chlorophyll characteristic of Lake Huron, the behavior is more like the second order recycle kinetics with its accelerated response to small loading changes.

This effect is quite important from a management point of view. The response of Lake Huron to small increases in total phosphorus loading is expected to be larger than strictly proportional. In fact the effect is more like a fourfold change in chlorophyll for a twofold change in phosphorus loading as shown in fig. 68a. The degree of reliability of these calculations under projected conditions is unknown at present. No verification of computational framework, in the sense of and independent computation of future widely different conditions and a check against field data, has been made. A two-fold difference in projected chlorophyll percent change exists between first order recycle kinetics and saturating kinetics (fig. 68a). Although saturating kinetics appear to be the probable mechanisms the sensitivity of the projections to this assumption is large and, therefore, this should be taken into account in utilizing these projections for management decisions.

The results of a more extensive series of simulations for increasing phosphorus loadings are shown in fig. 69. These calculations represent the results from the final calibrated model using the saturating recycle kinetics. An almost exponential increase is expected until 5 μg Chℓ-a/ℓ is reached, after which the increases are more proportional to increasing loading. These results clearly indicate that a positive feedback mechanism exists at low chlorophyll concentrations. As phosphorus load increases not only does total phosphorus concentration increase but the fraction of unavailable phosphorus decreases and the ratio of algal phosphorus to total phosphorus increases, compounding the increase in chlorophyll. For more eutrophic lakes this effect would not be observed since the recycle kinetics are saturated and behave as first order kinetics. However for Lake Huron, small increases in phosphorus loading produce significant changes in algal chlorophyll.

The effect of loading reductions to Lake Huron are examined based on various waste management alternatives as outlined by the IJC. These plans consist of removing 60%, 83%, and a theoretical 100% of the controllable phosphorus input to Lake Huron. This results in actual removals of 34.2%, 47.3%, and 57% respectively, of the total load assuming 43% of the input is from uncontrollable (non-point) sources. Effects of implementation of 80% phosphorus removal in the State of Michigan are also investigated as well as what type of waste load management is necessary to meet EPA's goal of nondegradation.

The results of these simulations are presented in table 15. The assumptions implicit in this analysis are: phosphorus load reductions are instan-

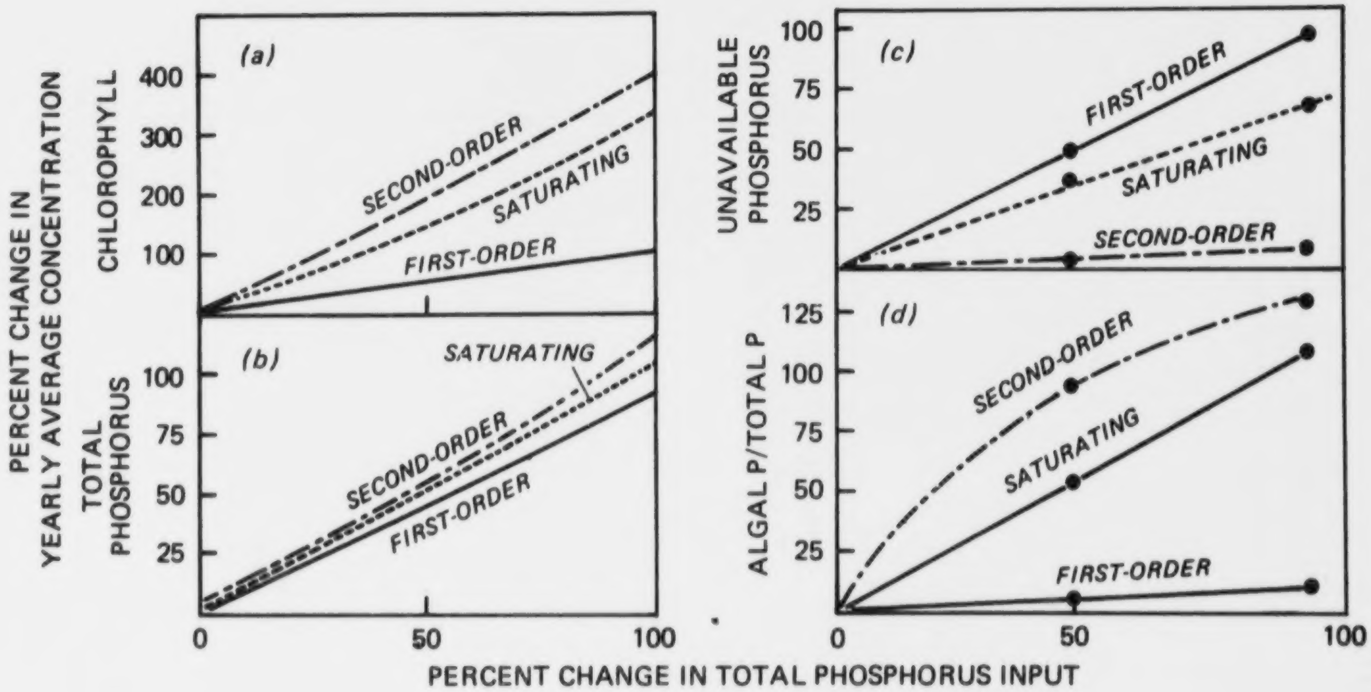


Figure 68. Effect of increases of phosphorus inputs to Southern Lake Huron. Percent change in yearly average epilimnion concentration versus percent change in total phosphorus input (a) Chlorophyll, $\underline{P}$; (b) Total phosphorus, p_T; (c) unavailable phosphorus, p_u; (d) Ratio of algal phosphorus to total phosphorus, P'/p_t.

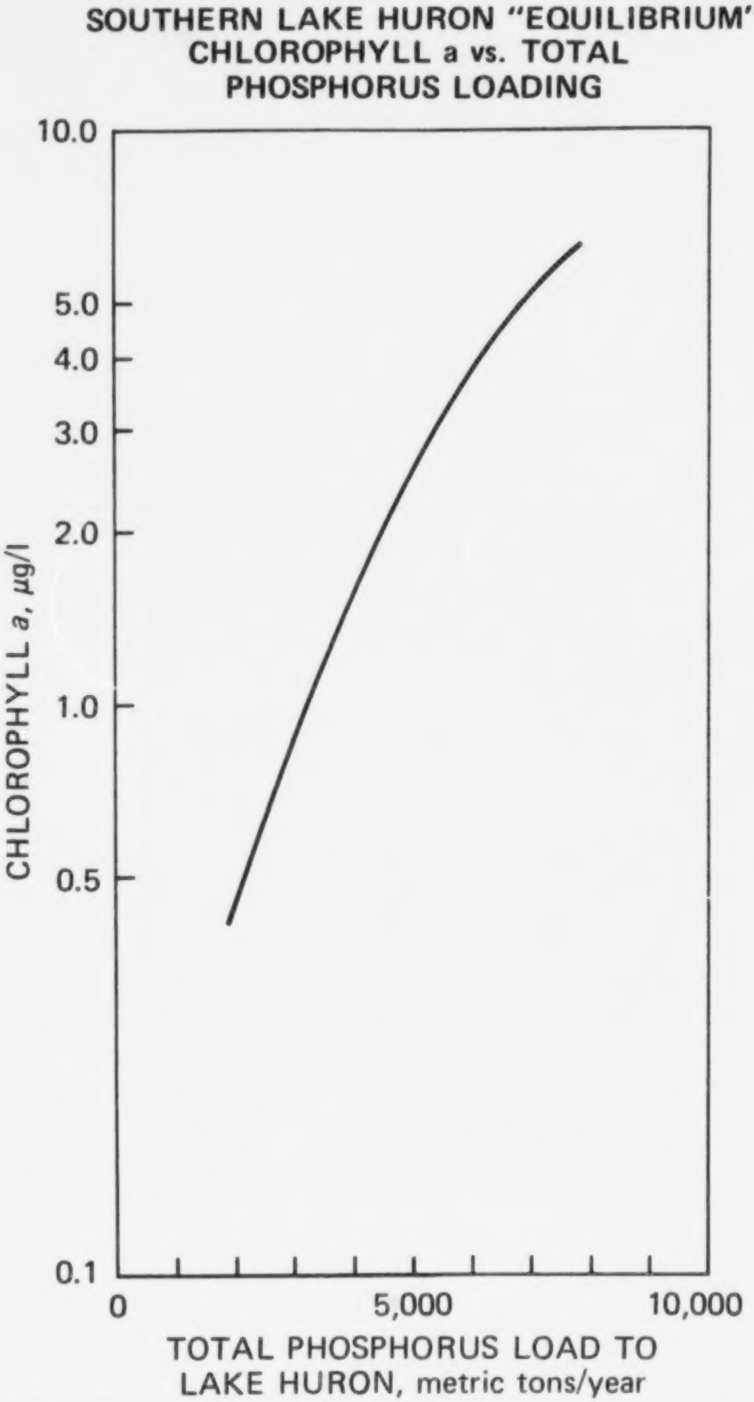


Figure 69. (Southern Lake Huron epilimnion) Yearly average chlorophyll concentration versus total phosphorus loading to Lake Huron.

TABLE 15. RESULTS OF MODEL SIMULATIONS

				SOUTHERN LAKE HURON			SAGINAW BAY		
SIMULATION	DESCRIPTION	SAGINAW BAY TOTAL P (Tonnes/Yr.)	LAKEWIDE TOTAL P LOAD (Tonnes/Yr.)	YEARLY AVG. Chℓ/a (µg/ℓ)	SPRING PEAK Chℓ/a (µg/ℓ)	YEARLY AVG. TOTAL P (µg P/ℓ)	YEARLY AVG. Chℓ/a (µg/ℓ)	SPRING PEAK Chℓ/a (µg/ℓ)	YEARLY AVG. TOTAL P (µg P/ℓ)
Base	Model Calibrated to 1974 Data	1,310	3,880	1.52	2.88	5.81	17.67	33.6	35.0
Non-Degradation	Maintain 1974 Yearly Avg. Chlorophyll	1,025	3,600	1.33	2.49	5.39	14.90	25.0	27.9
80%	80% Phosphorus Removal in Michigan	700	3,270	1.10	2.05	4.95	10.71	16.6	20.3
IJC60	34.2% Total Phosphorus Load Reduction to Saginaw Bay	860	3,430	1.21	2.27	5.16	13.25	20.7	23.9
IJC83	47.3% Total Phosphorus Load Reduction to Saginaw Bay	690	3,260	1.09	2.04	4.94	10.56	16.4	20.1
IJC100	57% Total Phosphorus Load Reduction to Saginaw Bay	560	3,130	1.00	1.91	4.79	8.51	13.6	17.4

taneous; the transport regime is the same as that used in the base run including the time variable flow from the Saginaw River and the bay-lake exchange; and relative fractions of available and unavailable phosphorus for the loadings remain the same as that used in the calibrated model. Since Saginaw Bay is sensitive to short term fluctuations because of its short hydraulic detention time these assumptions become important and since the actual changes to be expected in these phenomena are unknown over the period of the simulation, results presented for Saginaw Bay should be viewed with this in mind. The effects on Southern Lake Huron are important since they directly address the first and fourth reference questions of the Upper Lakes Reference Study: to what extent are the waters of Lake Huron being polluted on either side of the boundary to cause degradation of existing levels of water quality in the lake and what are the effects of preventative measures. These calculations enable one to gain some insight into these issues.

The results of the simulations indicate that the allowable phosphorus loading which maintains present water quality is 3600 tonnes/year. This will maintain a level of 1.31 μg/ℓ chlorophyll a in Southern Lake Huron epilimnion on a yearly average basis. Implementating an 80% phosphorus removal in Michigan yeilds levels of 1.1 μg Chℓ-a/ℓ in the southern lake as well as a 15% reduction in yearly averaged total phosphorus concentrations amounting to a decrease of 0.9 μg P/ℓ. The lowest concentrations result from the IJC plan which postulates a reduction for the Saginaw Bay load to 569 tonnes/yr.. Here chlorophyll a levels in Southern Lake Huron are held to 1.0 μg/ℓ after 15 years. There is also an accompanying 39% decrease in the peak spring chlorophyll as well as an 18% decrease in total phosphorus concentrations. Results in Saginaw Bay are most dramatic under this scheme showing an almost 50% reduction in yearly averaged chlorophyll a values to 8.5 μg/ℓ and a spring peak reduction to 13.5 μg/ℓ. Total phosphorus concentrations show a 50% reduction to 17 μg P/ℓ. More detailed results of these calculations are given in table 15.

It is important to emphasize that the absolute values of these projected concentrations are not certain to the three and four digits reported in the tables. The absolute error associated with these projections is unknown at present. Rather it is the relative changes that have more validity and it is these results that should be used as a guide in formulating the phosphorus reduction plans for Lake Huron and Saginaw Bay. An important issue that should be addressed in future work is the relative errors that can be associated with projections, that is what is the probable range of projected concentrations based on the present uncertainty of the mass discharges, the observed data, and the transport and kinetic parameters.

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TABLE A1. PHYTOPLANKTON GROWTH

Reaction Stoichiometric Equation

$$a_{pP}[PO_4\text{-}P] + a_{NP}\ (\alpha[NH_4\text{-}N] + (1-\alpha)[NO_3\text{-}N]) + a_{SiP}[Si] \xrightarrow{R_1} [Chl\text{-}a]$$

Reaction Rate

$$R_1 = K_1\theta_1{}^{T-20} r(I/I_s)\ \frac{[PO_4\text{-}P]}{K_{mP} + [PO_4\text{-}P]}\ \frac{[N]}{K_{mN} + [N]}\ [Chl\text{-}a]$$

Light Reduction

$$r(I/I_s) = \frac{ef}{K_e H}(e^{-\alpha_1} - e^{-\alpha_o})$$

$\alpha_1 = \alpha_o e^{-K_e H}$ K_e = extinction coeff. I_{av} = average daily solar radiation

$\alpha_o = I_{av}/fI_s$ f = photoperiod H = segment depth, T = temperature

Nitrogen Uptake

$[N] = [NH_4\text{-}N] + [NO_3\text{-}N]$ = Total Inorganic Nitrogen

$\alpha = [NH_4\text{-}N]/[N]$ = Ammonia fraction

Gross Primary Production

$G_{PP} = a_{CP}R_1$

with $r(\frac{I_{Lab}}{I_s}) = \frac{I_{Lab}}{I_s}\, e^{1-I_{Lab}/I_s}$

I_{Lab} = 115 ly/day = 30 kilolux [91]

TABLE A1 (continued)

Rate Constants Description	Notation	Value	Units
Saturated Growth rate @ 20°C	K_1	2.08	day^{-1}
Temperature coefficient	θ_1	1.068	none
Saturating Light Intensity	I_s	350.	ℓy/day
Half Saturation Constant for Phosphorus	K_{mp}	0.5	μgP/ℓ
Half Saturation Constant for Nitrogen	K_{mN}	25.0	μgN/ℓ
Carbon to Chlorophyll Ratio	a_{CP}	100.	μgC/μg Chl-a
Phosphorus to Chlorophyll Ratio	a_{pP}	0.5	μgP/μg Chl-a
Nitrogen to Chlorophyll Ratio	a_{NP}	10.0	μgN/μg Chl-a
Silica to Chlorophyll Ratio	a_{SiP}	50.0	μgSi/μg Chl-a
Phytoplankton Settling Velocity	W_p	0.05	m/day

TABLE A2. PHYTOPLANKTON RESPIRATION AND NON PREDATORY MORTALITY

Reaction Stoichiometric Equation

$$[\text{Chl-a}] \xrightarrow{R_2} a_{pP}(f_A[\text{PO}_4] + (1-f_A)[\text{Unavail PO}_4]) + a_{NP}(f_A[\text{NH}_4] + (1-f_A)[\text{Org-N}])$$

Reaction Rate

$$R_2 = K_2\theta_2^{T-20}\ [\text{Chl-a}]$$

Rate Constants Description	Notation	Value	Units
Endogenous Respiration Rate @ 20°C	K_2	0.05	day^{-1}
Temperature Coefficient	θ_2	1.045	none
Available fraction of respired phytoplankton	f_A	0.5	none

TABLE A3. HERBIVOROUS ZOOPLANKTON GROWTH

Reaction Stoichiometric Equation

$$[\mathrm{Chl\text{-}a}] \xrightarrow{R_3} \beta\, a_{CP}[Z_H] + (1-\beta)\ \{a_{NP}(f_A[\mathrm{NH}_4] + (1-f_A)[\mathrm{Org\ N}]) + a_{pP}\ (f_A[\mathrm{PO}_4] + (1-f_A)[\mathrm{Unavail\text{-}PO}_4])\}$$

Reaction Rate

$$R_3 = K_3 T \frac{K_{mg}}{K_{mg} + [\mathrm{Chl\text{-}a}]} [Z_H]$$

Assimilation Limitation

$$\beta = \frac{\varepsilon_H K_{m\varepsilon}}{K_{m\varepsilon} + [\mathrm{Chl\text{-}a}]}$$

Rate Constants Description	Notation	Value	Units
Filtering Rate	K_3	.136	ℓ/mgC/day-°C
Half Saturation Constant for Filtering Rate Limitation	K_{mg}	10.0	μg Chl-a/ℓ
Half Saturation Constant for Assimilation Rate Limitation	$K_{m\varepsilon}$	5.0	μg Chl-a/ℓ
Maximum Assimilation Efficiency	ε_H	0.6	none

TABLE A4. CARNIVOROUS ZOOPLANKTON GROWTH

Reaction Stoichiometric Equation

$$[Z_H] \xrightarrow{R_4} \varepsilon_c[Z_c] + (1-\varepsilon_c)\{a_{NC}\ (f_A[NH_4] + (1-f_A)[OrgN]) + a_{pC}\ (f_A[PO_4] + (1-f_A)[Unavail\text{-}PO_4])\}$$

Reaction Rate

$$R_4 = K_4 T[Z_H]$$

Rate Constants Description	Notation	Value	Units
Filtering Rate	K_4	0.096	ℓ/mgC/day-°C
Assimilation Efficiency	ε_c	0.6	none
Nitrogen to Carbon Ratio	a_{NC}	0.1	mgN/mgC
Phosphorus to Carbon Ratio	a_{pC}	0.005	mgP/mgC

TABLE A5. Zooplankton Respiration

Reaction Stoichiometric Equation

$$[Z] \xrightarrow{R_5} a_{NC}\ (f_A[NH_4] + (1-f_A)[Org\text{-}N]) + a_{pC}\ (f_A[PO_4] + (1-f_A)[Unavail\text{-}PO_4])$$

Reaction Rate

$$R_5 = K_5 \theta_5^{T-20}[Z]$$

Rate Constants Description	Notation	Value		Units
		Herbivorous	Carnivorous	
Respiration Rate @ 20°C	K_5	0.03	0.02	day^{-1}
Temperature Coefficient	θ_5	1.045	1.045	none

TABLE A6. NITRIFICATION

Reaction Stoichiometric Equation

$$[NH_4\text{-}N] \xrightarrow{R_6} [NO_4\text{-}N]$$

Reaction Rate

$$R_6 = K_6\theta_6^{T-20}\,[NH_4]$$

Rate Constants Description	Notation	Value	Units
Nitrification Rate @ 20°C	K_6	0.20	day^{-1}
Temperature Coefficient	θ_6	1.08	none

TABLE A7. MINERALIZATIONS

Specie	Reaction Stoichiometric Equation	Reaction Rate
Organic Nitrogen	$[\text{Org-N}] \xrightarrow{R_7} [\text{NH}_4\text{-N}]$	$R_7 = K_7\theta_7^{T-20} \frac{[\text{Chl-a}]}{[\text{Chl-a}] + K_{mr}}[\text{Org-N}]$
Unavailable Phosphorus	$[\text{Unavail-P}] \xrightarrow{R_8} [\text{PO}_4\text{-P}]$	$R_8 = K_8\theta_8^{T-20} \frac{[\text{Chl-a}]}{[\text{Chl-a}] + K_{mr}}[\text{Unavail-P}]$

Rate Constants Description		Value	Units
Organic Nitrogen Mineralization Rate @ 20°C	K_7	0.03	day^{-1}
Temperature Coefficient	θ_7	1.08	none
Unavailable Phosphorus Mineralization Rate @ 20°C	K_8	0.03	day^{-1}
Temperature Coefficient	θ_8	1.08	none
Half Saturation Constant for Nutrient Mineralization	K_{mr}	5.00	μgChℓ-a/ℓ
Settling Velocity for Organic Nitrogen	$W_{\text{Org-N}}$	0.05	m/day
Settling Velocity for Unavailable Phosphorus	$W_{\text{Unav-P}}$	0.05	m/day

TABLE A8. SYSTEM KINETIC DERIVATIVES

System	Parameter	
1	Phytoplankton Chlorophyll a	$d[Ch\ell\text{-}a]/dt = R_1 - R_2 - R_3$
2	Herbivorous Zooplankton Carbon	$d[Z_H]/dt = \beta a_{CP} R_3 - R_4 - R_{5H}$
3	Organic Nitrogen	$d[Org\text{-}N]/dt = a_{NP}(1-f_A)R_2 + (1-\beta)a_{NP}(1-f_a)R_3$ $+ (1-\varepsilon_c)a_{NC}(1-f_A)R_4 + a_{NC}(1-f_A)(R_{5H}+R_{5C}) - R_7$
4	Ammonia Nitrogen	$d[NH_4\text{-}N]/dt = - a_{NP}\alpha R_1 + a_{NP}f_A R_2 + (1-\beta)a_{NP}f_A R_3$ $+ (1-\varepsilon_c)a_{NC}f_A R_4 + a_{NC}f_A(R_{5H}+R_{5C}) - R_6 + R_7$
5	Nitrate Nitrogen	$d[NO_3\text{-}N]/dt = - a_{NP}(1-\alpha)R_1 + R_6$
6	Unavailable Phosphorus	$d[Unavail\text{-}P]/dt = a_{pP}(1-f_A)R_2 + (1-\beta)a_{pP}(1-f_A)R_3$ $+ (1-\varepsilon_c)a_{pC}(1-f_A)R_4 + a_{pC}(1-f_A)(R_{5H}+R_{5C}) - R_8$
7	Available Phosphorus	$d[PO_4\text{-}P]/dt = - a_{pP}R_1 + a_{pP}f_A R_2 + (1-\beta)a_{pP}f_A R_3$ $+ (1-\varepsilon_c)a_{pC}f_A R_4 + a_{pC}f_A(R_{5H}+R_{5C}) + R_8$
8	Carnivorous Zooplankton	$d[Z_c]/dt = \varepsilon_c R_4 - R_{5C}$
9	Available Silica	$d[S_i]/dt = - a_{SiP}R_1$

TABLE A9. TIME VARIABLE SAGINAW BAY WASTE LOADINGS

Time (days)	[Org N] (lbs/day)	Time (days)	$[NH_4\text{-}N]$ (lbs/day)	Time (days)	$[NO_4\text{-}N]$ (lbs/day)
0	36,100	0	3,890	0	45,200
1	36,100	2	3,890	1	45,200
3	19,700	18	1,900	8	24,400
20	18,900	21	7,640	24	207,000
29	175,000	28	22,000	28	515,000
30	125,000	32	12,000	30	258,000
38	34,900	38	4,220	39	66,700
44	14,800	49	2,270	53	73,700
56	70,900	52	3,940	59	92,500
59	19,500	56	10,500	65	406,000
66	187,000	59	8,680	74	128,000
84	26,000	65	38,100	90	66,200
86	53,800	73	11,000	95	230,000
96	143,000	80	9,290	101	127,000
100	87,400	87	4,660	106	127,000
114	36,800	94	11,700	112	44,600
134	41,200	95	1,960	137	69,000
141	169,000	101	4,140	141	118,000
147	35,100	105	8,060	142	99,400
193	18,000	109	1,990	170	44,200
206	5,410	119	3,700	179	10,000
227	19,000	123	7,140	189	9,280
255	8,040	134	5,340	207	2,990
295	945	135	11,000	225	2,520
311	16,450	141	1,060	261	3,960
325	6,850	142	10,800	280	4,990
353	7,880	143	1,140	353	4,240
365	7,880	155	3,090	365	4,240
		162	6,910		
		165	3,180		
		172	3,180		
		226	1,020		
		261	4,900		
		352	5,710		
		365	5,710		

(continued)

TABLE A9 (continued)

Time (days)	[Unavail-P] (lbs/day)	Time (days)	[PO_4-P] (lbs/day)	Time (days)	[Si] (lbs/day)
0	4,060	0	2,710	0	94,000
1	4,060	3	2,710	1	94,000
16	2,570	18	637	18	46,700
24	14,700	21	2,510	21	111,000
29	54,300	22	3,550	23	338,000
32	12,200	24	4,300	25	216,000
34	3,830	25	4,910	28	324,000
49	1,830	28	8,970	29	687,000
56	8,210	30	2,150	32	164,000
59	9,920	32	3,350	38	76,600
66	65,600	36	1,840	39	115,000
67	21,500	49	957	50	47,400
74	6,470	56	3,310	53	230,000
90	4,630	59	2,930	59	169,000
95	24,900	64	9,320	65	767,000
99	11,200	67	4,160	74	251,000
114	7,960	78	1,400	78	188,000
134	3,990	99	818	93	265,000
141	37,600	100	9,540	95	444,000
142	14,300	101	2,400	101	41,500
147	5,520	106	701	105	271,000
154	3,380	109	2,530	114	75,600
162	11,200	126	975	120	72,600
165	4,870	134	3,280	130	92,400
206	1,840	135	639	134	70,200
295	774	141	529	137	246,000
311	2,800	142	1,710	147	91,100
337	249	153	364	158	42,800
365	1,650	155	1,550	162	91,100
		158	609	176	53,200
		162	2,690	179	32,200
		165	1,000	186	83,400
		176	646	274	40,700
		193	1,100	295	30,900
		226	706	311	65,800
		262	871	325	35,900
		274	2,090	353	34,800
		280	1,330	365	34,800
		295	1,800		
		305	1,870		
		311	4,770		
		317	1,820		
		325	2,020		
		337	917		

TABLE A10. MAIN LAKE HURON WASTE LOADINGS

Segment	[Org-N]	[NH_4-N]	[NO_3-N] (lbs/day)	[Unavail-PO_4]	[PO_4-P]	[Si]
1	53,266	81,786	215,503	5,473	2,218	681,661
2	46,394	42,438	127,158	6,086	1,744	51,867

TABLE A11. BOUNDARY CONCENTRATIONS

System	Parameter	Segment	Boundary Concentration
1	Phytoplankton chlorophyll	1	.1
		2	.1
		3	25.0

TABLE A12. FLOWS

TO (Segment)	FROM (Segment)	FLOW (cfs)
1	boundary	175,460
2	1	2,000,460 (north-south circulating flow)
2	boundary	6,555
2	3	11,235 (Day 0 - 151) 1,561 (Day 181-365)
boundary	2	193,250 (Day 0 - 151) 183,576 (Day 181-365)
3	boundary	11,235 (Day 0 - 151) 1,561 (Day 181-365)
1	2	1,825,000 (north-south circulating flow)

TABLE A13. EXCHANGES

$(10^6 FT^3/DAY)$

Time (day)	Segment Interface 4-1	Segment Interface 5-2	Segment Interface 2-1	Segment Interface 5-4	Segment Interface 3-2
0	415,385	134,769	4.32	13.51	2592.
30	415,385	134,769	4.34	13.51	2592.
60	415,385	134,769	4.34	13.51	2592.
90	415,385	134,769	4.34	13.51	6912.
120	415,385	134,769	4.34	13.51	6912.
150	415,385	134,769	4.34	13.51	6912.
180	415,385	134,769	4.34	13.51	6912.
210	0	0	4.34	13.51	6912.
240	0	0	4.34	13.51	2592.
270	0	0	4.34	13.51	2592.
300	415,385	134,769	4.34	13.51	2592.
330	415,385	134,769	4.34	13.51	2592.
360	415,385	134,769	4.34	13.51	2592.
365	415,385	134,769	4.34	13.51	2592.

TABLE A14. SEGMENT PARAMETERS

Parameter	Segment 1	Segment 2	Segment 3	Segment 4	Segment 5
Depth (m)	15.0	15.0	6.0	50.0	50.0
Extinction Coefficient $K_e (m^{-1})$	0.237	0.271	1.5	0.237	0.271

TABLE A15. TIME VARIABLE FUNCTIONS

Time (days)	Temp (Seg 1) (°C)	Temp (Seg 2) (°C)	Temp (Seg 3) (°C)	Temp (Seg 4) (°C)	Temp (Seg 5) (°C)	I_{av} langleys/day	f
0	1.34	1.68	1.00	1.25	1.19	100.	0.37
114	1.34	1.68	3.00	1.25	1.19	388.	0.56
141	3.56	6.75	12.90	2.47	2.96	520.	0.60
173	9.94	12.78	21.50	4.63	5.37	627.	0.64
204	13.83	18.16	20.20	4.43	4.64	600.	0.63
239	16.33	18.29	19.50	4.53	7.55	488.	0.57
274	14.52	16.56	17.30	5.05	4.71	320.	0.50
303	11.62	13.61	13.75	5.98	4.85	180.	0.44
336	5.98	5.86	2.25	5.54	6.39	108.	0.37
365	1.34	1.68	1.00	1.25	1.19	100.	0.37